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# Productivity and carbon budgets of harvested Central Appalachian forests

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# **Productivity and Carbon Budgets of Harvested Central Appalachian Forests**

**Sarah C. Davis**

Dissertation submitted to  
Eberly College of Arts and Sciences  
at West Virginia University  
in partial fulfillment of the requirements  
for the degree of

Doctor of Philosophy  
in  
Environmental and Evolutionary Biology

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Morgantown, WV  
2007

Keywords: forest productivity, timber harvest, land use, carbon sequestration, nitrogen saturation

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# **ABSTRACT**

## **Productivity and Carbon Budgets of Harvested Central Appalachian Forests**

**Sarah C. Davis**

Land conversion and industrial pollution are two of the most influential vehicles for anthropogenic perturbation of natural terrestrial processes and both have increased dramatically over the course of the last century. This research explores the role of Central Appalachian hardwood forests in the global carbon (C) balance during a century of regeneration with changing land use and atmospheric pollution. Most of the forests in this region were logged in the early 1900s. During the century that followed, nitrogen (N) deposition rates became especially high in parts of Central Appalachia where an increasing number of regenerated mature forests are now undergoing N saturation. I explored the effects of N saturation on processes that control productivity using a model that I modified to reflect conditions associated with Stage 2 of N saturation. I then applied the model to forests that have experienced different harvest histories during the last century of forest re-growth. I found that carefully planned harvests, such as diameter-limit cutting and single tree selection cutting, can stimulate ecosystem productivity by as much as 37%. To determine the regional contribution of mature forests to atmospheric C sinks, I assessed the spatial variability of foliar and soil N concentrations and applied the validated productivity model to sites across the state of West Virginia. Generally, I found that over the century of regeneration following harvest, forests in the Central Appalachian region sequestered an average of 4 to 5 Tg C yr<sup>-1</sup>. The modeled estimate of carbon storage is stimulated up to 20% by N saturation, a process that varies in intensity across the state and may be correlated with a transition in tree species composition. Loss of these forests would add about 300 Tg C to the atmosphere that would take another century to recover.

**This work is dedicated to**

**Jeanne Horn and Christine Davis**

**(my roots)**

## **ACKNOWLEDGEMENTS**

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# **PRODUCTIVITY AND CARBON BUDGETS OF HARVESTED CENTRAL APPALACHIAN FORESTS**

by

**Sarah C. Davis**

## Chapter 1

### INTRODUCTION

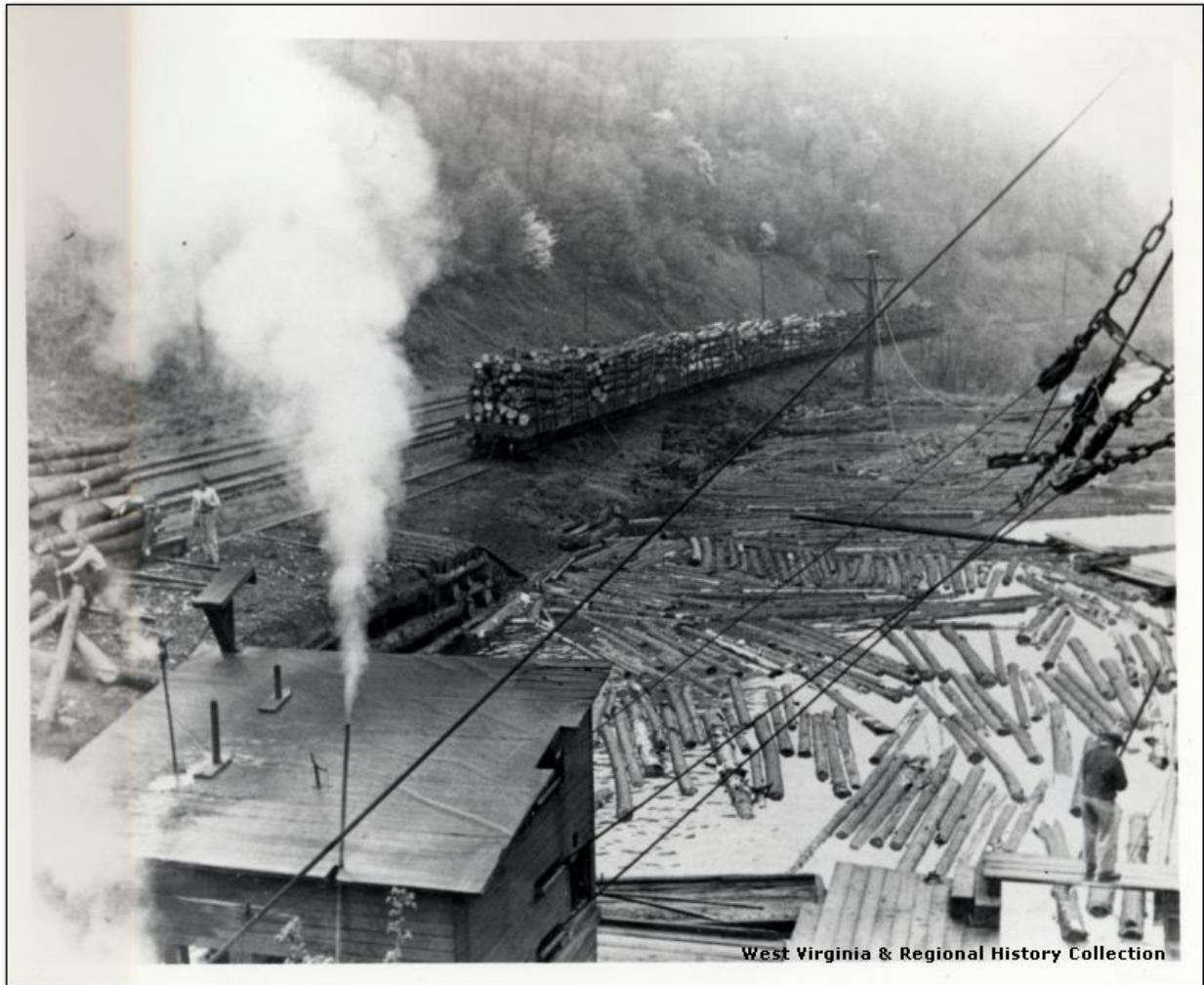


Photo of Cass Mill in early 1900s archived by West Virginia and Regional History Collection, West Virginia University Libraries

The main objective of my dissertation research is to advance the understanding of processes that control productivity of forest ecosystems in the Central Appalachian region of the eastern United States. Forests are an important component of the global carbon balance and can act as both sinks and sources of atmospheric carbon dioxide. Current estimates of the global terrestrial sink of CO<sub>2</sub> from the atmosphere equate to approximately 0.1Pg C yr<sup>-1</sup> (Denman et al. 2007). It has recently been suggested that land use conversion is the primary cause for this sink (Caspersen et al. 2000, Houghton et al. 2003). Rising atmospheric CO<sub>2</sub> concentrations and increased nitrogen (N) deposition rates, both from fossil fuel emissions, also potentially contribute to growth stimulations that may enhance carbon (C) sequestration by terrestrial processes. The combined effects of these processes on forest carbon budgets have lead to debate over historic and future roles of forests in the global carbon balance (Denman et al. 2007). My research explores the role of Central Appalachian hardwood forests in the global carbon balance during a century of regeneration.

There have been many studies that have tried to quantify forest C sequestration at a regional scale (Wofsy et al. 1993, Heath et al. 1993, Schimel 1995, Houghton 1999, Schimel et al. 2000, Pacala et al. 2001, and House et al. 2002, Houghton 2003), but the Central Appalachian region is under-represented in the datasets that inform estimates of C in the eastern United States. Few studies have compiled detailed measurements of forests in West Virginia (which represent a large portion of the Central Appalachian ecosystem) to make regionally-accurate estimates of forest productivity (Schuler 2004, Jenkins et al. 2001). Forests are very important resources in West Virginia and are engrained in the history of the state. At the turn of the last century, most of the state was forested with old-growth tulip poplar and white oak (Figure 1.1) surrounding smaller portions of land that were in pasture at the time (Hicks 1998). Between 1903 and 1911, almost all of the forestland was harvested for wood products that were removed from the region (Trimble 1977). The population density has remained low enough over the last century so that



the majority of land in West Virginia regenerated with relatively little disturbance. By the year 2000, the U.S.D.A. Forest Service estimated that 12 million acres (48590 km<sup>2</sup>) or 77% of the land in WV was marketable timberland (Griffith and Widmann 2003). Most of this land is mature saw-timber, recent values of which are shown in Table 1.1, and most of the forestland is also privately owned (Griffith and Widmann 2003).

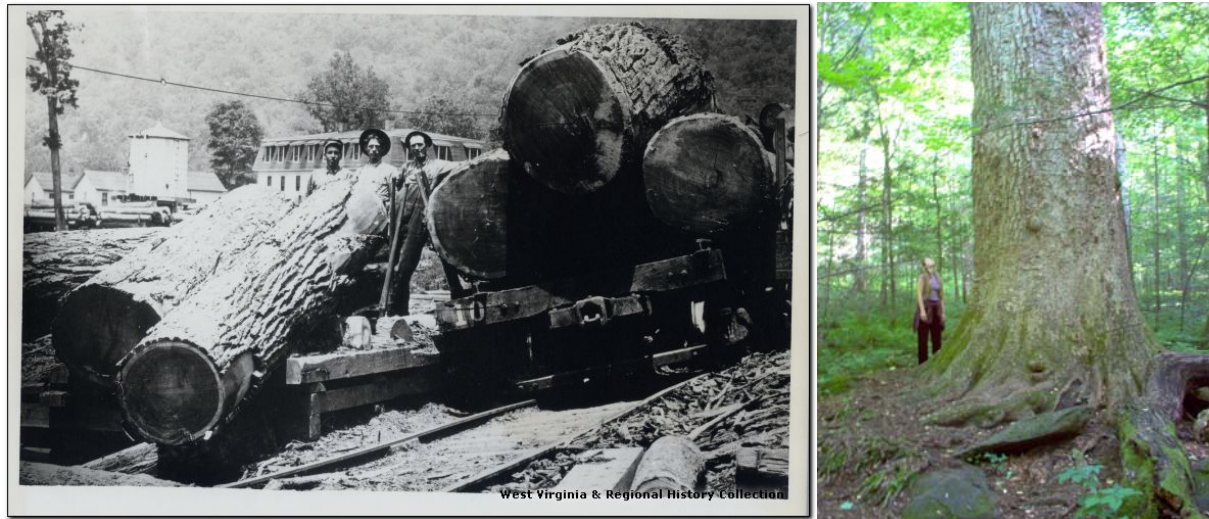


Figure 1.1 Historical photograph of logging tulip poplar in the early 1900's from the West Virginia and Regional History Collection (left) and a photograph of the author in the only remaining virgin tulip poplar stand on public land in the eastern U. S. taken in 2006 in South Carolina (right).

My research addresses the amount of carbon that is stored in forests of West Virginia that are likely to be harvested in the near future. My research also contributes to understanding the role of land use change in the global carbon balance. All of the valuable timber species listed in Table 1.1 are dominant canopy hardwood species in West Virginia. The forests in this area have been classified as mixed mesophytic forests by Braun (1950) and were dominated by oak and hickory species after large-scale chestnut mortality in the 1930's. More recently forests in the state have also been classified as beech-maple-birch dominated (Hicks 1998). The state of West Virginia actually lies at an ecological transition zone between oak-hickory dominant and beech-maple-birch dominant forests (Iverson and Prasad 2001). If the progression of climate change induces species range shifts (Parmesan and Yohe, 2003), my research may be a valuable

contribution to understanding this transition zone and the consequence of range shifts for ecosystem carbon budgets.

Table 1.1. Recent prices for dominant timber species in WV (Northeastern Research Station Research Note NE-385). Mbf = 1000 ft of board 12" wide and 1" thick

Timber Species	Price per Mbf
Red oak	\$855
Poplar	\$395
Cherry	\$1560
Hard maple	\$1116
Soft maple	\$666

In addition, my research addresses the changing N conditions of forests in the region due to historically high rates of N deposition. The Fernow Experimental Forest in Parsons, WV is managed by the U.S.D.A. Forest Service and portions have symptoms of N saturation (Peterjohn et al. 1996). There has been a surge of recent literature that explores the consequences of N saturation for ecosystem processes and the Fernow has most recently been identified as an example of a Stage 2 N-saturated ecosystem (Stoddard 1994, Aber et al. 1998, Jenkins et al. 2005). Stage 2 of N saturation is defined as the condition of the ecosystem after prolonged inputs of nitrogen when nitrification and nitrogen leaching remain high year-round, foliar N increases, and soil cations decline (Aber et al. 1998, Jenkins et al. 2005). There are no ecosystem productivity models that incorporate processes associated with this advanced stage of the N saturation. Because a model is required to estimate regional productivity and carbon sequestration, this is the first challenge that I will focus on in my research.

The over-arching question that I aim to address in this dissertation is: How much carbon is stored in Central Appalachian forests of West Virginia and how much will the carbon pool change in response to future land use? First, I will determine if an ecosystem productivity model can be applied and validated for forests of West Virginia. This stage of the research involves (a) parameterizing a model for a mature 100-year-old forest in the Fernow, (b) calibrating the model

to reflect N-saturated processes of the forest, and then (c) testing the accuracy of the model by validating it against on-site measurements. Second, I will determine if the validated ecosystem productivity model can accurately predict productivity responses to harvesting events. In this case, I will test the model performance by (a) simulating four different harvest histories that have been documented by the Forest Service in different watersheds of the Fernow and (b) comparing the modeled productivity in response to these harvest events to on-site measurements of productivity that were compiled with dendrochronologic techniques. With a working model validated for the region and harvest events, one can attain preliminary estimates of the relative impact of different harvesting practices on net ecosystem productivity and carbon sequestration.

Spatial variation of ecosystem processes can influence the accuracy of regional predictions (Reich et al. 1999, Jenkins et al. 1999, Pan et al. 2004). Thus, the third stage of my research involves describing the spatial variation of N concentrations across West Virginia. To accomplish this goal, I compared the canopy foliar N and soil N concentrations associated with dominant canopy trees along an elevation gradient in the Fernow to canopy foliar N and soil N concentrations associated with dominant canopy trees across the statewide elevation gradient in West Virginia. Once the spatial variation has been described, then the final step toward answering my main research question is to apply the validated ecosystem productivity model to forested sites across West Virginia and use the model to estimate carbon sequestration rates statewide.

To more concisely summarize the objectives, I will:

- 1) describe and validate an ecosystem productivity model for a Central Appalachian forest,
- 2) test the accuracy of the validated model for simulating different harvest histories,
- 3) compare and contrast the variation of N concentrations at two spatial scales in West Virginia, and



- 4) apply the ecosystem productivity model to forests across West Virginia to determine the range and average carbon storage capacity of forests in the Central Appalachian region.

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## Chapter 2

### **Productivity of nitrogen-saturated forests in the Central Appalachian region: an adaptation of the PnET-CN model**



## ABSTRACT

Recent advances in ecosystem process descriptions associated with nitrogen-saturated forests allowed us to revise and improve a model of ecosystem productivity to reflect nitrogen saturation. We identified nitrogen retention, nitrification, and nitrogen use efficiency as processes that could be improved in the PnET-CN model. We compared the performance of PnET-CN with a new model version, PnET-CN<sub>sat</sub> by contrasting model outputs with on-site measurements in a 100-year-old nitrogen-saturated watershed in the Fernow Experimental Forest. PnET-CN<sub>sat</sub> outperformed the original model, and the average discharge of N predicted over a 20 year period was only 19% higher than the total discharge of N over the same period. Regional estimates of forest productivity and terrestrial carbon sequestration have generally overlooked variable N availability as a vector for forest growth changes. Assimilating new findings about N-saturated ecosystem processes should improve regional estimates of ecosystem change in response to N saturation and other anthropogenic influences. PnET-CN<sub>sat</sub> provides an improved description of ecosystem productivity with N fluxes that are characteristic of forests in later stages of N saturation.

## 1. Introduction

Forest ecosystem productivity is strongly coupled to ecosystem nitrogen balances. Despite the recent pervasion of models that describe terrestrial productivity and carbon sequestration, processes that control nitrogen cycling in these models are often poorly developed or not included at all. There is a broad spectrum of nitrogen availability found among forests in temperate regions that has been difficult to address experimentally in the past. With recent advances in our understanding of a variety of processes that control ecosystem nitrogen balances, there is an opportunity to amass collective scientific discoveries to form a coherent description of nitrogen processes that affect nutrient cycling of forest ecosystems showing symptoms of nitrogen saturation.

Literature that addresses forest nitrogen balances and processes controlled by varying degrees of nitrogen availability have mounted in recent years (Swank and Vose 1997, Aber et al. 1998, Fenn et al. 1998, Lovett and Rueth 1999, Aber et al. 2002, Lovett et al. 2002, Ollinger et al. 2002, Campbell et al. 2004, Gilliam et al. 2005, Templer et al. 2005), but the majority of ecosystem process models primarily describe the nitrogen-limited extreme of the nitrogen availability spectrum. Nitrogen limitations on productivity are important and may become increasingly more important for biotic systems as atmospheric CO<sub>2</sub> increases (Hungate et al. 2003; Luo et al. 2004; Finzi et al. 2006; Reich et al. 2006). On the other hand, deposition of N from anthropogenic emissions is increasing N availability in some forested regions (Fenn et al. 1998) and therefore contributes to a dichotomy of forest nitrogen conditions that may have equally important but opposing implications for ecological productivity (Nadelhoffer et al. 1999).

Of the comprehensive nitrogen cycling models currently published, few address the nitrogen dynamics inherent to a nitrogen-saturated ecosystem (Townsend et al. 1996, Aber et al. 1998, Fenn et al. 1998, Gilliam et al. 2001, Jenkins et al. 2005) and most of these do not link N

cycling processes to processes that control productivity. Jenkins et al. (2005) described a theoretical model of how forest nitrogen cycling changes with increasing stages of N saturation. Gilliam et al. (2001) summarized the soil calcium and aluminum concentrations that are associated with a gradient of soil N conditions in addition to changes in soil N transformations with sucrose and amino acid additions. Fenn et al. (1998) provided a general review of the relative changes in nitrogen forms as a forest progresses through N saturation that Aber et al. (1998) presented a revised conceptual model of N saturation to include foliar N changes and consequences for carbon assimilation. Townsend et al. (1996) described both the N and C cycling responses to N deposition using the Nitrogen Deposition and Ecosystem Production (NDEP) model. Each of these studies presents a conceptual model for changing ecosystem processes across varied N conditions, but only the NDEP model attempts a mathematical description of these changes by relying on C:N ratios of different components in the ecosystem.

Ecosystem process models that estimate productivity and are designed for wide geographical applications are valuable for comparing relative nutrient balances among ecosystem types, but are practically limited to ecosystems with similar characteristics and nutrient cycling dynamics. Substantial modifications may be required before such models can be applied to forests with nutrient pools and fluxes that lie outside the range of processes for which the original model was validated. The PnET suite of models (Aber and Federer 1992, Aber et al. 1995, Aber et al. 1997, Aber et al. 2002) has been applied to ecological questions of forest productivity in a large number of studies with the intention to use PnET as a tool to calculate productivity estimates for a wide range of forest types. Early versions of PnET estimate forest growth processes based on carbon and water balances that are easily verifiable in watersheds with long-term historical data records. The PnET-CN version of this model suite builds on earlier versions by including nitrogen balances that are integral to forest growth (Aber et al. 1997, Ollinger et al. 2002). PnET-CN was validated in several forests across the northeastern U.S. and



has elegantly addressed forest productivity differences associated with a variety of anthropogenic pollutants and management activities. Despite these successes, the application of PnET-CN to nitrogen-saturated forests, such as the Fernow Experimental Forest in Parsons, WV, USA (Peterjohn et al. 1996), has produced marginal results (Hom et al. 2006).

This study contributes to the empirical development of a widely used ecosystem process model by testing the validity of PnET-CN productivity and nitrogen outputs against direct measurements of the same variables in a 100-year-old nitrogen-saturated watershed in the Fernow Experimental Forest. We developed a new version of the model, PnET-CN<sub>sat</sub>, by modifying quantitative descriptions in the model for nitrogen cycling dynamics that have been found to be important in empirical studies of nitrogen balances in nitrogen-saturated forests. Finally, we tested PnET-CN<sub>sat</sub> against productivity and N concentrations measured in the nitrogen-saturated watershed in the Fernow Experimental Forest for validation.

## **2. Review of PnET-CN model**

### *2.1 Model development*

The first version of the PnET model was introduced in 1992 as a simple generalized process model that described the carbon and water balances that control forest productivity (Aber and Federer 1992). In this model, gross photosynthesis was predicted based on canopy foliar N concentrations and a generalized linear relationship between foliar N and photosynthetic rates. Gross photosynthesis was calibrated according to site specific environmental conditions and historical records of on-site climate variation that determine water availability to plants. Plant respiration was assumed to be a fraction of gross photosynthesis that would also vary with climatic conditions. Photosynthesis and respiration were scaled through canopy layers according to incremental reductions in light penetration with increasing depth from the top of the canopy. On-site radiation variability was included in climate records to parameterize the maximum light

environment at the top of the canopy. The difference between canopy photosynthesis and canopy respiration yielded an estimate of aboveground net primary productivity. The model runs on a monthly time-step, which was determined to be as accurate as a daily time-stepped version of the model (Aber et al. 1996). Belowground biomass allocation and climate change scenarios were added to the model routines in 1995 (Aber et al. 1995). A nitrogen cycling routine was added in the PnET-CN version to more completely describe ecosystem nutrient cycling and responses to N deposition or fertilization (Aber et al. 1997). Subsequent developments of the PnET model have involved hybridization with nutrient cycling models such as Biome-BGC and DNDC (Gbondo-Tugbawa et al. 2001, Li et al. 2000, Stange et al. 2000).

## 2.2 Nitrogen budget model in PnET-CN

The PnET-CN model (Aber et al. 1997, Ollinger et al. 2002) defines an initial pool of nitrogen in a forest ecosystem that is available for new ecosystem processes as a percentage of nitrogen in decaying matter. This N pool is allocated to mineralization, immobilization, plant uptake, or leaching with a net loss of N from year to year (Figure 2.1A). The proportion of nitrogen released from decomposing organic matter is calculated on a monthly time-step and becomes the estimate of gross mineralization. The proportion of mineralized nitrogen that is immobilized (NReten) is determined by the equation

$$NReten = (NImmobA + NImmobB * SoilPctN) / 100$$

where NImmobA and NImmobB are constants defined to approximate a linear fit of a complete range of immobilization proportions that correspond to a given soil N concentration (SoilPctN). This range from 0 to 1 is assumed to correspond to soil organic matter (SOM) nitrogen percentages that range from 4.3% N to 1.5% N. Accordingly, the value of 151 is assigned for NImmobA and -35 is assigned for NImmobB in all forest types for which the original model was validated so that complete immobilization of N occurs when there is 1.5% N in SOM and no

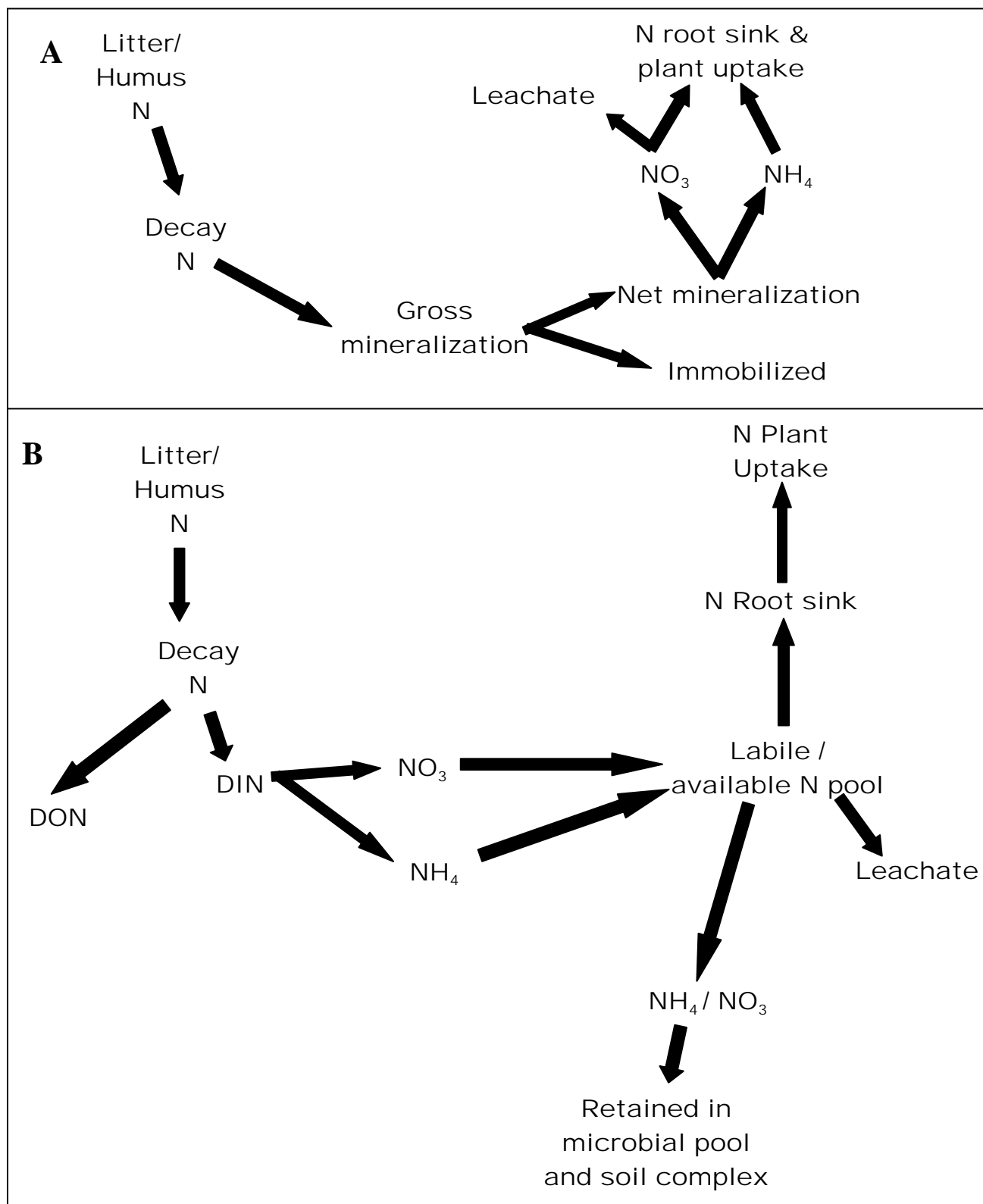


Figure 2.1. Conceptual diagram of soil (A) N cycle in PnET-CN (derived from Aber et al. 1997) and (B) N cycle as modified in this study for PnET-CN<sub>sat</sub> model to describe N-saturated forests. The new model distinguishes the dissolved inorganic nitrogen (DIN) pool from dissolved organic nitrogen (DON) that results from decaying matter. Nitrification rates are also defined as a site specific percentage of overall mineralization such that NO<sub>3</sub><sup>-</sup> pools are appropriately assigned to labile N pathways.

immobilization occurs when there is 4.3% N in SOM. The N that is not immobilized is allocated for plant uptake from pools of mineralized  $\text{NO}_3^-$  and  $\text{NH}_4^+$ . The proportion of the mineralized pool that becomes  $\text{NO}_3^-$  (NRatioNit) is defined according to the equation

$$\text{NRatioNit} = ((\text{NRatio} - 1) \text{FolConRange})^2,$$

where FolConRange is the range of foliar nitrogen variability in the forest canopy from year to year and NRatio is a coefficient for plant N demand. NRatio is controlled strictly by plant N pools according to the equation

$$\text{NRatio} = 1 + ((\text{PlantN}/\text{MaxNStore}) * \text{FolConRange})$$

where PlantN is the total N pool in plant matter and MaxNStore is the maximum amount of N in plant matter. Nitrate that is not allocated for plant uptake is lost from the overall N pool through leaching. A more detailed description of the equations that describe nitrogen budgets in PnET-CN is outlined in Aber et al. (1997).

The nitrogen relationships described above are linked to the carbon budget of the forest as well through the photosynthesis vs. foliar N relationship. Unlike previous versions of PnET, foliar N concentrations are predicted by PnET-CN based on the plant N pool in a given year with the equation

$$\text{BudN} = (\text{BudC} / \text{CFracBiomass}) * \text{FLPctN} * (1 / \text{FolNRetrans}) * \text{Nratio}$$

where BudC is carbon in buds, CFracBiomass is the fraction of carbon in total biomass, FLPctN is the minimum nitrogen concentration in foliar litter and FolNRetrans is the proportion of nitrogen that is retranslocated.

### 2.3 The problem with PnET-CN N-cycling

Contrary to the carbon balance of the PnET-CN model structure, the above N-cycling equations do not necessarily reflect specific ecosystem processes but instead assign values that suit a particular range of N concentrations. A consequence of this “black box” type of

approximation is that, over a time sequence, all of the available nitrogen becomes depleted from the modeled forest system reflecting nitrogen limitation that occurs in mature forests. Thus, the nitrogen budget described above was validated for several forests in the northeastern U.S. (Aber et al. 1997). However, these equations may not be an accurate reflection of N cycling in nitrogen-saturated forest ecosystems. Specifically, we might expect the labile soil N pools of an N-saturated system to vary outside the normal ranges observed in other temperate ecosystems. There are an increasing number of studies published that describe the changes in proportions of labile N pools with N saturation and variable fates of N in such systems (Gilliam et al. 2001, Christ et al. 2002, Davidson et al. 2003, Campbell et al. 2004, Templer et al. 2005, Jenkins et al. 2005). Mechanistic descriptions are still rare but we can introduce empirical descriptions of N-cycling from recently published literature that we will then test in a new N cycling routine to determine if these new relationships improve the predictive power of PnET-CN for a wider range of N availability.

### **3. Application of new findings related to N saturation**

#### *3.1 Empirical evidence of N-cycling processes in N-saturated forests*

To reconstruct a nitrogen cycle that reflects recently published characteristics and processes of nitrogen-saturated forests, we first built a skeleton of mathematical relationships that should be defined for any ecosystem nitrogen cycle (Paul and Clark 1996, Schlesinger 1997). At this initial stage of development, we identified essential components of the nitrogen cycle that were previously missing from the PnET-CN framework. Specifically not addressed in PnET-CN were (1) the proportion of total dissolved nitrogen that becomes inorganic nitrogen and (2) the chelation of nitrogen in soil aggregates. In PnET-CN, all dissolved N was assumed to be inorganic and plant available. Inorganic nitrogen pools have recently been reported for nitrogen-saturated forests as approximately 20% of the total dissolved nitrogen pool (Templer et

al. 2005). The total inorganic nitrogen retained in nitrogen-saturated forests has also been recently reported by Campbell et al. (2004) as 44% of nitrogen input in the Fernow Experimental Forest. This retention estimate includes chelation by soil particles as well as microbial immobilization. Abiotic retention of N is still not completely understood, so this is an important parameter that should be specified according to forest site. This site-specific retention parameter also accounts for any additional nitrogen that may be acquired through microbial activity, as has been observed but poorly quantified (Davidson et al. 2003).

We made several other modifications to PnET-CN based on measurements and descriptions of nitrogen cycling processes that have been published specifically for nitrogen-saturated forests (Peterjohn et al. 1996, Aber et al. 1998, Fenn et al. 1998, Gilliam et al. 2001, Campbell et al. 2004, Jenkins et al. 2005). These changes included (1) site specific nitrification rates, (2) reduced seasonal fluctuation in N leachate, and (3) nitrogen allocated for new bud growth.

We identified the method of generating nitrification rates as a limitation of the N cycle in the original PnET-CN model because predictions of nitrification are based on plant N pools instead of soil processes. With nitrogen saturation, the plant N pools would remain but soil N transformations are likely to change. Nitrification rates are typically much higher in nitrogen-saturated ecosystems but vary site to site, so we included a site-specific nitrification percentage based on measurements made in the Fernow Experimental Forest by Gilliam (2001) and confirmed in several other studies (Christ et al. 2002, Campbell et al. 2004).

The original PnET-CN model assumed a strong seasonal fluctuation in dissolved nitrogen output as is often observed in N-limited ecosystems. This fluctuation is controlled by plant N demand that is much higher during the growing season. On the other hand, a reduction in the seasonality of N leachate has been observed repeatedly in N-saturated forests, and this has been used as an identifying characteristic to define Stage 2 of N saturation (Stoddard 1994, Fenn et

al. 1998, Aber et al. 1998, Jenkins et al. 2005). To our knowledge, however, no mechanistic descriptions of seasonal leaching patterns in N-saturated forests have been published. We modified the retention and leaching equations of PnET-CN to reflect a more modest seasonal fluctuation in dissolved nitrogen output (Peterjohn et al. 1996, Aber et al. 1998, Jenkins et al. 2005) by using a generic algorithm that proportionally redistributes excess labile nitrogen throughout the year. More specifically, in our modified model half of the N is retained during the first four months of the year and this nitrogen is released during the growing season months. Then in the last two months of the year, during early winter months, half of the leachable nitrogen is again retained. While the mechanism that controls this seasonal retention is unknown, the equations serve as a testable hypothesis for the generalized proportions of leachate and are based on repeated observations.

In order to correct for the imbalance in nitrogen allocated to foliage when nitrogen is highly available, our final revision of PnET-CN involved modifying the equation that describes nitrogen in tree buds (BudN), as described in section 2.2 above. In PnET-CN, foliar N is estimated as a proportion of bud N such that when there is highly available nitrogen, this equation over-predicts the proportion of N allocated to leaves. Retranslocated N is already applied to the plant N pool in the model so the second allocation of retranslocated N to BudN allows the foliar N estimate to become inflated. This inflation of foliar N is magnified with lower proportions of retranslocated N during senescence and drives model predictions outside normal biological ranges of foliar N. To correct for this, we rewrote the equation for BudN as

$$\text{BudN} = (\text{BudC} / \text{CFracBiomass}) * ((1.3 * \text{FLPctN}) * \text{NRatio})$$

and thus, the entire foliar pool of nitrogen is not recycled each year; instead a proportional amount of litterfall N is allocated for BudN.

### *3.2 Comparing the new conceptual N-cycling model to the original*

Figure 2.1 depicts the conceptual model of N-cycling in PnET-CN and our modified version, PnET-CN<sub>sat</sub>, based on process differences that we have described. The differences in the new model can be summarized as follows:

- Dissolved nitrogen inputs are divided into organic and inorganic pools (Templer et al. 2005).
- Inorganic N is partitioned into  $\text{NO}_3^-$  and  $\text{NH}_4^+$  according to site-specific nitrification rates (Gilliam et al. 2001, Christ et al. 2002, Campbell et al. 2004).
- Total inorganic soil N retention is specified for the site to account for N in soil aggregates and additional microbial inputs (Campbell et al. 2004).

Other changes to the N cycle that are not shown in this conceptual diagram include

- reduced seasonal fluctuation in N leachate (Peterjohn et al. 1996, Aber et al. 1998, Jenkins et al. 2005) and
- nitrogen allocated for new bud growth.

We retained the original equations for soil organic matter input to the N cycling subroutine as well as the output routines that allocate nitrogen back to the plant N pool in the system.

## **4. Comparison of model performance: PnET-CN vs. PnET-CN<sub>sat</sub>**

### *4.1 Parameterizing model runs*

We tested three different modelling methods against on-site measurements of five output variables in a 100-year-old nitrogen-saturated watershed of the Fernow Experimental Forest. The Fernow is located in a mixed mesophytic portion of the Appalachian Plateau (Braun 1950) where extensive logging took place between the years of 1903 and 1911 (Trimble 1977). The local climate is fairly rainy and cool with an average maximum temperature of 15°C and about 146 cm of rainfall spread evenly throughout the year (Kochenderfer 2006). The watershed is comprised



of mixed hardwoods that have been regenerating since the early 1900s and is located at 695 to 790 meters in elevation with a generally northeast aspect. All model runs included the same site specific climate records and climate change scenarios. Climate data was available for the site starting in 1952, and climate was reconstructed for the years prior to 1952 using monthly averages. All model runs started in 1900, included a 70% biomass removal in response to logging in 1908 and 25% biomass removal in response to the Chestnut Blight in 1935. No harvesting or disturbance has been documented since those events. Atmospheric CO<sub>2</sub> was gradually ramped up to 380 ppm from 280 ppm in 1950 and N deposition was ramped up to concentrations reported in 2000 by the National Atmospheric Deposition Program ([nadp.sws.uiuc.edu](http://nadp.sws.uiuc.edu)) from the baseline value starting in 1940.

Seventeen site-specific input parameters were applied to the model runs according to on-site field measurements or previously measured data (Table 2.1). The same parameters were used in each model run, except for two input parameters, Nitr and NReten, which only apply to the new PnET-CN<sub>sat</sub> model run. Data for all measured parameters were collected during the growing season of 2006. Soil and litter variables were collected monthly from May through September in six plots randomly located in the 100-year-old watershed. Three samples were obtained from each plot and then homogenized. Woody and leafy litter components were separated for analysis of N content. All soil and litter samples were dried for 48 hours at 65°C, ground in an amalgamator for 20 seconds and then wrapped in tin for analysis through Dumas combustion in a Carlo Erba CN autoanalyzer (CE Instruments, Milan, Italy). The minimum N concentration observed in foliar litter and woody litter over the five month sampling period was applied as the minimum foliar litter [N] (FLPctN) and the minimum woody litter [N] (WLPctN) respectively. Soil organic matter N (HON) was estimated from average [N] in soil samples collected over the growing season.

Table 2.1. Model parameters used in comparative model runs. Local climate data were used for each site and included measured precipitation, temperature, and radiation records starting in 1949 and reconstructed back to 1900.

Modelling method	Input parameter	Value	Source of estimate	Definition
PnET-CN and PnET-CN <sub>sat</sub>	AmaxA	41.1	Reich et al. (1998)	Intercept of foliar N vs. A <sub>max</sub> relationship
	AmaxB	42.3	Reich et al. (1998)	Slope of foliar N vs. A <sub>max</sub> relationship
	SLWmax	73	measured on site 2002, 2006	Minimum Specific leaf weight at the top of the canopy
	GDDFolStart	340	Hicks, unpublished	Sum of degrees above 0 before leaf growth
	GDDFolEnd	960	Hicks, unpublished	Sum of degrees above 0 at end of leaf growth
	GDDWoodStart	507	Hicks, unpublished	Sum of degrees above 0 before wood growth
	GDDWoodEnd	3045	Hicks, unpublished	Sum of degrees above 0 at end of wood growth
	Latitude	39	measured	Latitude of site
	WHC	7	from Christ et al. (2002)	Water holding capacity
	FLPctN	0.01512	measured on site 2006	Minimum N concentration in leaf litter
	WLPctN	0.00877	measured on site 2006	Minimum N concentration in woody litter
	MaxNStore	76	Adams et. al. (2004)	Maximum N in plant pool
	FolNRetrans	0.5	measured on site 2006	Percent of N retranslocated from leaves
	NRatio	1.9	from Peterjohn et al. (1996)	Mobile N ratio to maximum plant N
	HON	451	measured on site 2006	N in humus organic matter
PnET-CN <sub>sat</sub>	NReten	0.44	Campbell et al. (2004)	Proportion of inorganic N retained in soil
Only	Nitr	0.92	Gilliam et al. (2001)	Nitrification:mineralization ratio

Specific leaf weight of the top canopy leaves (SLW<sub>max</sub>) was calculated from canopy foliage that was collected from dominant canopy trees using a shotgun in July of 2002 (N = 22) and 2006 (N=25). These tree species included *Acer saccharum*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Prunus serotina*, and *Quercus rubra*. The N concentration of canopy foliage was also measured using the same drying, amalgamation, wrapping, and combustion procedures described above. Canopy foliar N is not an input in PnET-CN or PnET-CN<sub>sat</sub> (it is predicted as an output in the models and was used as a validation measurement).

#### 4.3 Validation data

The validation test of each model run included a comparison of modelled output variables to on-site measurements of aboveground net primary productivity (ANPP), historical stream [N], historical streamflow, foliar [N], and woody litter [N] collected from Watershed 13 (WS 13) in the Fernow Experimental Forest. Litterfall collections from a near-by watershed, in combination with on-site tree-ring data, were combined to estimate ANPP of this 100 year-old watershed. Species-specific allometric equations were used to estimate aboveground biomass at annual increments from tree ring analysis (Tritton and Hornbeck 1982, Brenneman et al. 1978).

Historical records of streamflow and stream N concentrations in the watershed were obtained from USDA Forest Service public datasets (unpublished data, Northeastern Research Station). Streamflow records were only recorded for 15 years in WS 13, so we also compared model outputs to the long-term streamflow record of a near-by watershed (WS 4) that has also been maintained as an un-harvested forest. Some differences exist in the hydrology of the two watersheds, so a validation against both watersheds is a more robust test of modeled streamflow predictions. Canopy foliage of the dominant tree species was sampled with a shotgun in 2002 (N

= 22) and 2006 (N = 25). These tree species included *Acer saccharum*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Prunus serotina*, and *Quercus rubra*. Leaf tissue was dried for 48 hours at 65°C, ground, and analyzed for N in a Carlo Erba CN autoanalyzer (CE Instruments, Milan, Italy) using the Dumas combustion method. The average N concentration of woody litter samples collected monthly as described above (N = 30) was used as a validation test against modeled estimates of woody litter [N]. It should be noted that this is independent of the input parameter WLPctN, which specifies the MINIMUM wood litter N concentration that was measured over the entire growing season. Model estimates of foliar and woody litter N concentrations for the last five years of the model run were averaged and compared to the on-site measurements of foliar [N] and woody litter [N]. Methods for estimating foliar [N] and woody litter [N] were compared using a one-way ANOVA (SAS-JMP software version 5.1).

#### 4.4 Results of original model

In the first model run, we fully parameterized the original PnET-CN model to include site-specific carbon, water and nitrogen balance parameters in the Fernow Experimental Forest (Table 2.1). Overall, in this scenario, the model showed a poor validation with measured ecosystem attributes of the N-saturated forest. Contrary to measurements of stream N, PnET-CN predicted that no nitrogen was leached from the watershed over the past 20 years (Figure 2.2A). Modelled foliar N was 19% and 38% greater than foliar N measured in 2002 and 2006, respectively and the long-term foliar N estimates over 103 years modeling were 36% and 58% greater than measured foliar N in 2002 and 2006 (Figure 2.3). On the other hand, modelled woody litter N was not significantly different from measured woody litter N ( $F = 1.5203$ ,  $p = 0.2320$ ) and thus, was the only nitrogen variable that showed a good validation using PnET-CN

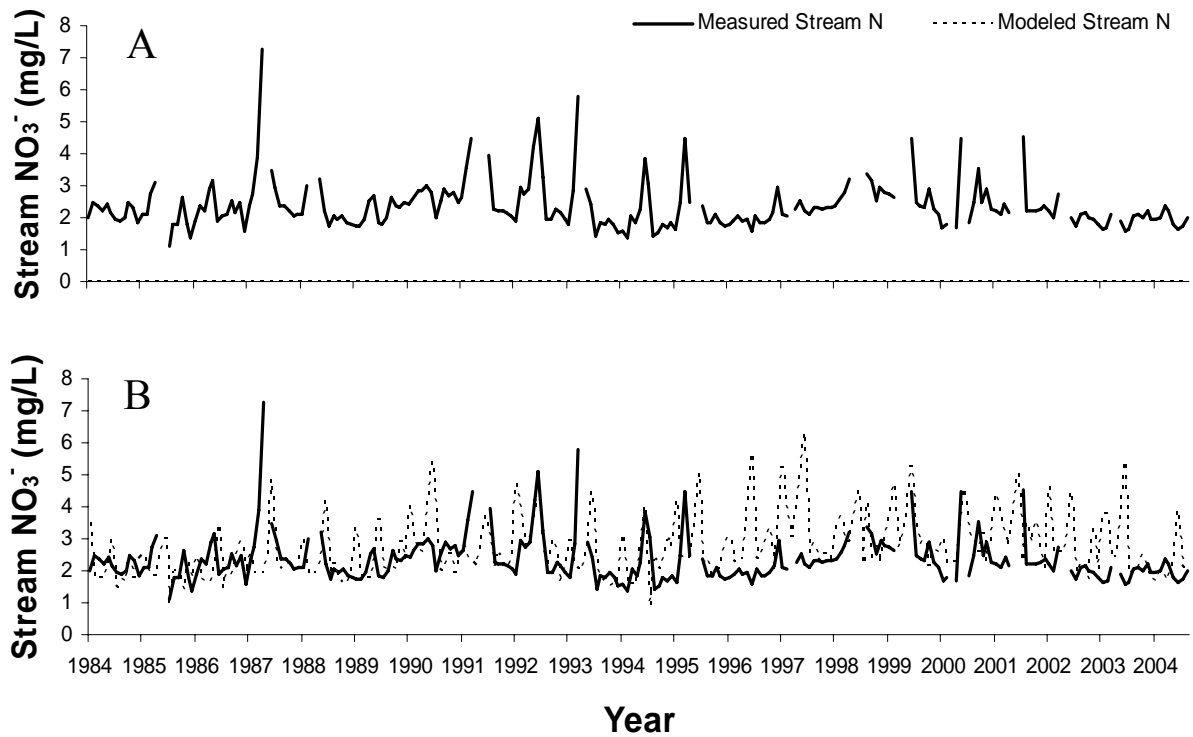


Figure 2.2. Measured (solid) and modelled (dashed) estimates of  $\text{NO}_3$  in streamflow in a 100 year-old watershed in the Fernow Experimental Forest (Parsons, WV). Modelled estimates were generated using using PnET-CN with full on-site parameterization including its original N balance subroutine (A), and using PnET-CN<sub>sat</sub> with full on-site parameterization including a modified N balance subroutine (B); PnET-CN predicted no  $\text{NO}_3$  was leached over 20 years, but regression of measured estimates on PnET-CN<sub>sat</sub> modelled estimates over a 20 year period was significant ( $r^2 = 0.03$ ,  $p = 0.0067$ ).

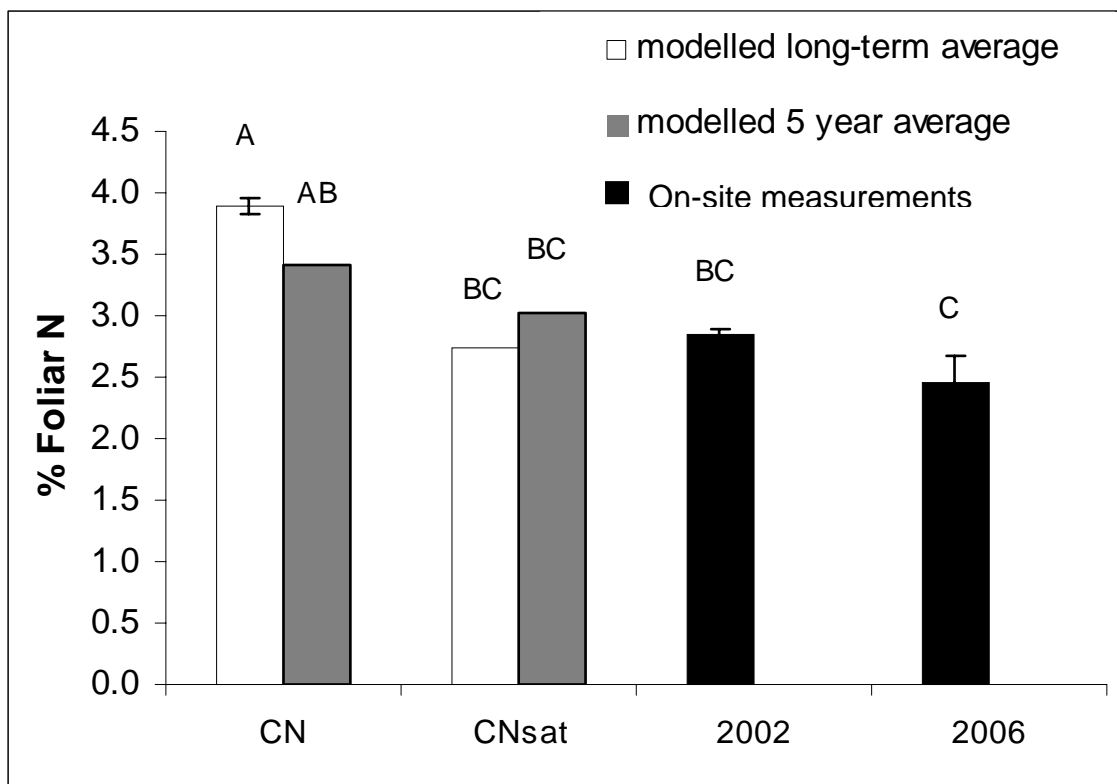


Figure 2.3. Measured (solid) and modelled (striped) estimates of canopy foliage N concentration in a 100 year-old watershed in the Fernow Experimental Forest (Parsons, WV). Modelled estimates represent means of output for the last 5 years modelled and were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (CN N param), and using PnET-CN<sub>sat</sub> with full on-site parameterization including a modified N balance subroutine (CNsat). Measured estimates reflect means of foliar N concentration of sun leaves collected from the five dominant tree species in the Fernow watershed during 2002 and 2006. Bars denoted by different letters are significantly different according to a one-way ANOVA with  $\alpha = 0.05$  (SAS-JMP software version 5.1).

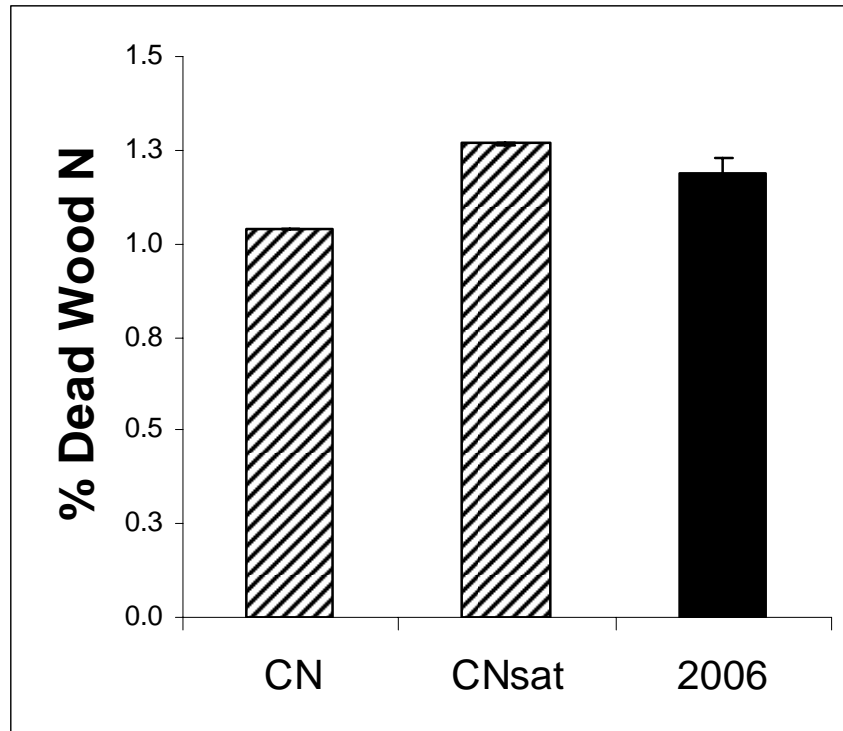


Figure 2.4. Measured (solid) and modelled (striped) estimates of % N in woody litter in a 100 year-old watershed in the Fernow Experimental Forest (Parsons, WV). Modelled estimates represent means of output for the last 5 years modelled and were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (CN N param), and using PnET-CN<sub>sat</sub> with full on-site parameterization including a modified N balance subroutine (CNsat). The measured estimate reflects mean woody litter N concentration collected in the watershed in 2006. There were no significant differences among means according to a one-way ANOVA with  $\alpha = 0.05$  (SAS-JMP software version 5.1).

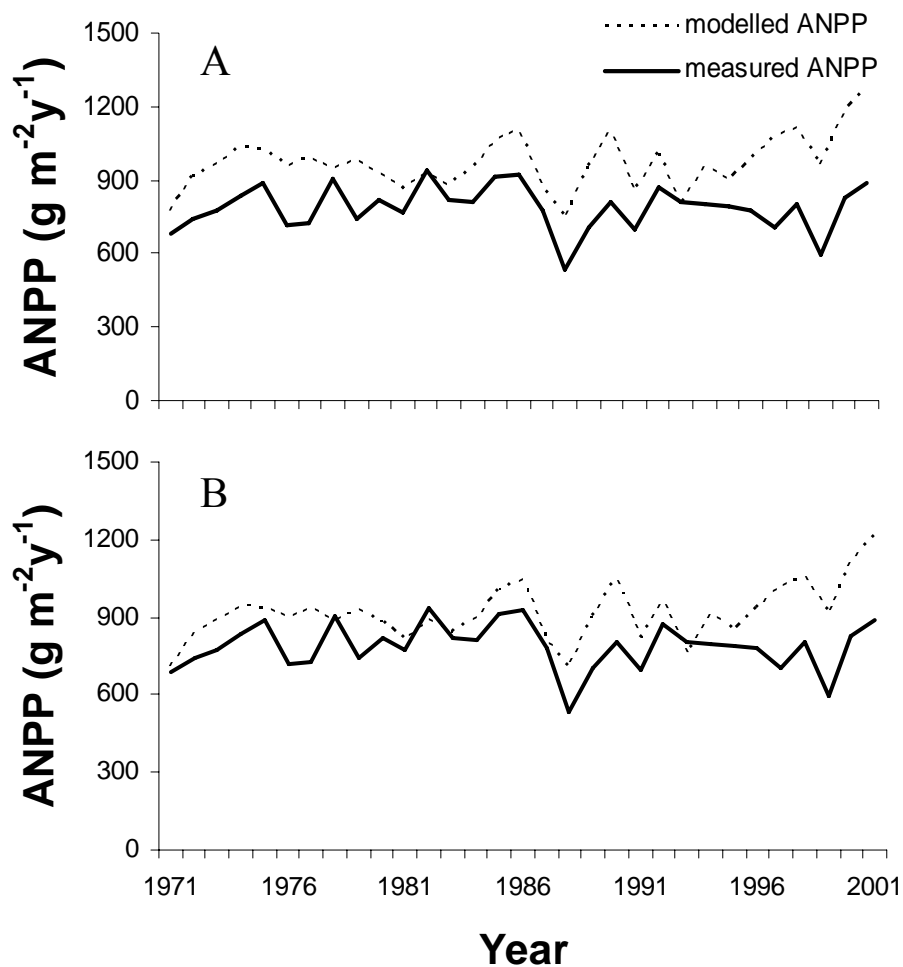


Figure 2.5. Measured (solid) and modelled (dashed) estimates of aboveground net primary productivity (ANPP) in a 100 year-old watershed in the Fernow Experimental Forest (Parsons, WV). Modelled estimates were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (A), and using PnET-CN<sub>sat</sub> with full on-site parameterization including a modified N balance subroutine (B).



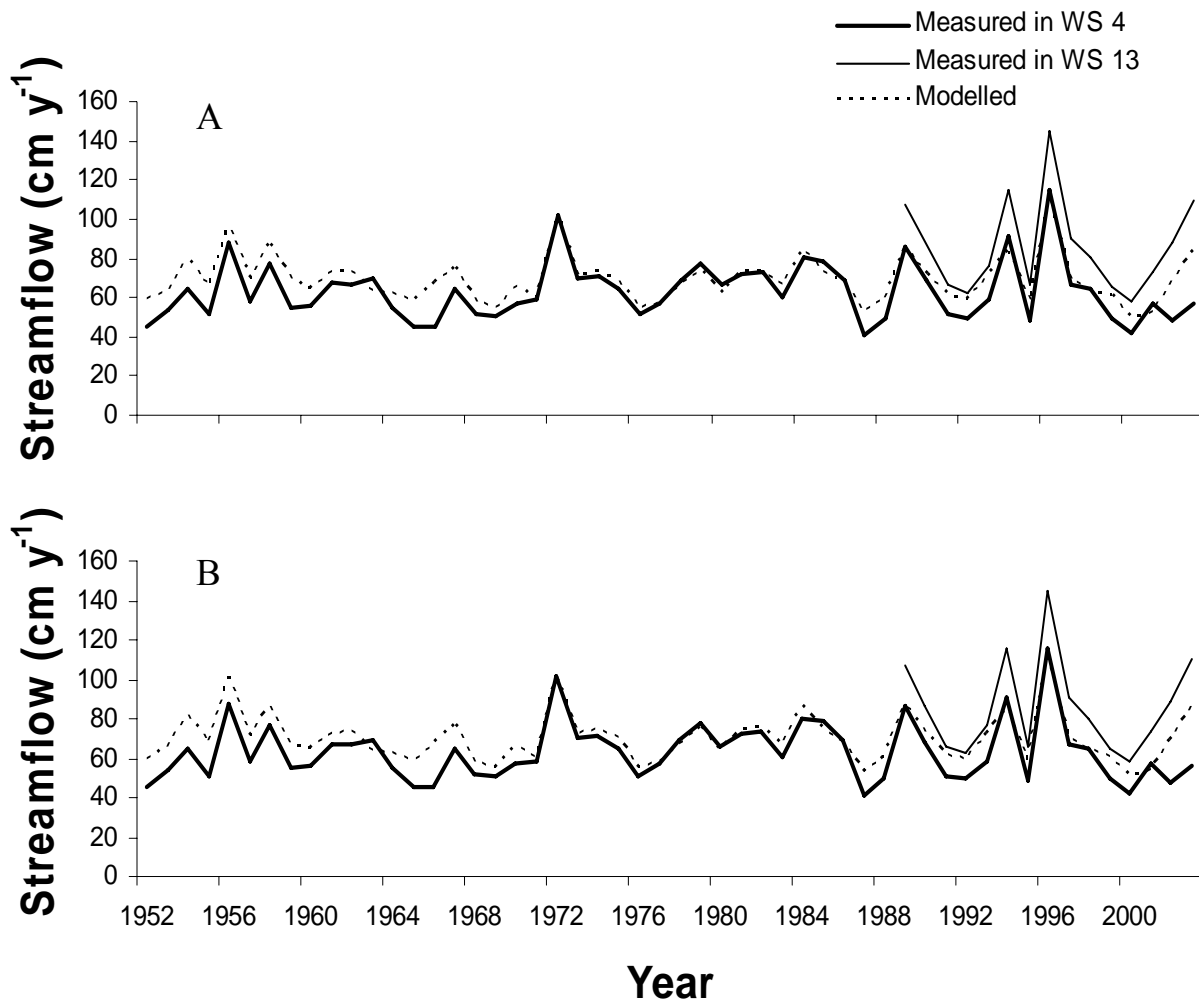


Figure 2.6. Measured (solid) and modelled (dashed) estimates of N in streamflow in a 100 year-old watershed in the Fernow Experimental Forest (Parsons, WV). Modelled estimates were generated using PnET-CN with full on-site parameterization including its original N balance subroutine (A), and using PnET-CN<sub>sat</sub> with full on-site parameterization including a modified N balance subroutine (B). Regressions of measured estimates against PnET-CN and PnET-CN<sub>sat</sub> modelled estimates over a 20 year period were significant (PnET-CN vs. WS 4:  $r^2 = 0.76$ ,  $p < 0.0001$ ; PnET-CN<sub>sat</sub> vs. WS 4:  $r^2 = 0.76$ ,  $p < 0.0001$ ; PnET-CN vs. WS 13:  $r^2 = 0.93$ ,  $p < 0.0001$ ; PnET-CN<sub>sat</sub> vs. WS 13:  $r^2 = 0.93$ ,  $p < 0.0001$ ).

in this N-saturated forest (Figure 2.4). PnET-CN over-estimated ANPP by 24% averaged over a 30-year period (Figure 2.5A) even though the relationship between measured ANPP and modeled ANPP was significant ( $R^2=0.25$ ,  $p = 0.0046$ ). Stream flow estimates from PnET-CN accurately reflected the measured stream flow since 1952 and modeled and measured data were significantly correlated (WS 4:  $r^2 = 0.76$ ,  $p < 0.0001$ ; WS 13:  $r^2 = 0.93$ ,  $p < 0.0001$ ; Figure 2.6A).

The equations that describe soil N balances in PnET-CN become an evident source of error when applying the model to a nitrogen-saturated watershed. The error is inflated primarily because nitrogen is not gradually depleted in a nitrogen-saturated system, and secondarily because high nitrification rates are likely to change the balance between plant uptake and nitrogen leaching in a forest with high nitrogen availability (Peterjohn et al. 1996, Aber et al. 1998; Fenn et al. 1998, Jenkins et al. 2005). Using PnET-CN, the modelled nitrogen pool was depleted rapidly because the high nitrate supply was drained from the system.

#### 4.5 *Results of the revised model: PnET-CN<sub>sat</sub>*

We fully parameterized the modified model, PnET-CN<sub>sat</sub>, to include site-specific carbon, water and nitrogen balance parameters in the Fernow Experimental Forest (Table 2.1). This included two site specific parameters (NReten and Nitr; Table 2.1) not used in the parameterization of the original PnET-CN. PnET-CN<sub>sat</sub> estimates of all five output variables were validated against on-site measurements. The average stream NO<sub>3</sub><sup>-</sup> leached over 20 years was 19% higher than average measured NO<sub>3</sub><sup>-</sup> leached (Figure 2.2B) and there was a significant correlation of measured and modelled stream NO<sub>3</sub><sup>-</sup> ( $R^2 = 0.03$ ,  $p = 0.0067$ ). Foliar N (Figure 2.3) and woody litter N (Figure 2.4) concentration estimates from PnET-CN<sub>sat</sub> were not significantly different from measurements made in the forest ecosystem. A five year average of foliar N using PnET-CN<sub>sat</sub>

was 6% higher than the measured foliar N in 2002 and 23% higher than 2006 measurements and the long-term foliar N average over the 103 years modelled was 4% lower and 11% higher than 2002 and 2006 foliar N measurements respectively (Figure 2.3). PnET-CN<sub>sat</sub> modelled woody litter N concentration was only 7% greater than the woody litter [N] measured in 2006 (Figure 2.4). In addition, ANPP was on average 17% higher than on-site tree-ring estimates (Figure 2.5B) and there was a significant correlation of measured and modelled ANPP ( $R^2 = 0.24$ ,  $p = 0.0053$ ). Streamflow estimates from PnET-CN<sub>sat</sub> accurately reflected the measured streamflow since 1952 (Figure 2.6B) and modeled and measured data were significantly correlated (WS 4:  $r^2 = 0.76$ ,  $p < 0.0001$ ; WS 13:  $r^2 = 0.93$ ,  $p < 0.0001$ ).

## **5. Discussion and Conclusions**

PnET-CN<sub>sat</sub> is a new version of the PnET model that more accurately predicts variables associated with forest carbon and nitrogen balances than PnET-CN in nitrogen-saturated forest ecosystems. However, site specific nitrification and N retention must be assessed for the forested sites to which this model version is applied. This model is most appropriate for forests that are in Stage 2 of the nitrogen saturation process when biologically available nitrogen is excessive year round and nitrification occurs all year as well (Aber et al. 1998, Fenn et al. 1998, Jenkins et al. 2005). PnET-CN<sub>sat</sub> more accurately estimated the three validation parameters than the original PnET-CN model version. PnET-CN<sub>sat</sub> more comprehensively describes ecosystem N balances that contribute to productivity changes and, thus, can be used to further develop hypotheses about N processes that are not well understood in nitrogen-saturated forests.

The primary uncertainty of PnET-CN<sub>sat</sub> is how the model deals with reduced seasonal fluctuation in dissolved nitrogen output that is observed in N-saturated forest ecosystems.

Peterjohn et al. (1996) estimated that seasonal variability in stream N discharge was reduced in Stage 2 of N saturation to state with a 20% coefficient of variation, but no mechanistic descriptions of the seasonal reduction have been quantified. Several theoretical hypotheses have been proposed for what is occurring with this nitrogen pool. One potential explanation is the loss of N to the atmosphere through volatilization, a process that has been identified as increasing in the most advanced stages of N saturation (Aber et al. 1998, Jenkins et al. 2005). Neilsen et al. (2001) found that volatilization and release of  $N_2O$  is greater immediately following soil thaw and it stands to reason that an atmospheric N sink would increase in the early winter season when temperature fluctuations are likely to induce short freeze-thaw periods more frequently than during other times of the year. Because of the large percentage of N that is retained, we suggest that there may be more than one pathway for the additional nitrogen retention. Aber et al. (1998) identified three classes of soil processes that are likely explanations for N retention under high nitrogen conditions; two of these processes involve organic nitrogen accumulation by microbial activity. Tree and understory species composition changes over time may also affect nitrification and leaching processes (Fenn et al. 1998, Lovett and Rueth 1999, Lovett et al. 2002, Templer et al. 2005), but these probably have less of an influence on seasonal dynamics than microbial community changes. In addition, fungal species can dominate heterotrophic nitrification processes so they may be key regulators of the available soil nitrogen pools. Schimel et al. (1984) observed that the potential for heterotrophic nitrification was higher than that of autotrophic nitrification in forests. Duggin et al. (1991) found that heterotrophic and autotrophic processes were equally important for controlling nitrification in forests. Pedersen et al. (1999) found that autotrophic nitrification can be more important in recently clear-cut forests, but heterotrophic processes dominate nitrification in mature forest ecosystems. Little is known

about seasonal fluctuation of soil microbial biomass in temperate deciduous forests, but North et al. (1997) found that standing crops of hypogaeal fungi increased in the fall season while consumption by animals was low and that consumption resumed in the winter period. If higher trophic level organisms increase consumption of fungal nitrogen in the early winter season, they may also export that nitrogen through emigration.

There are increasing numbers of forested sites in the Eastern U.S. that are considered nitrogen-saturated (Jenkins et al. 2005). Regional estimates of forest productivity and terrestrial carbon sequestration have generally overlooked variable N availability as a vector for forest growth changes. Such large scale estimations will become even more inaccurate as nitrogen saturation spreads across the region due to anthropogenic nitrogen sources. The PnET-CN<sub>sat</sub> model successfully employed processes that have been described for nitrogen-saturated forests in recent literature. By assessing site-specific N retention and nitrification, Stage 2 of N saturation may be addressed with this model.

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## **Chapter 3**

### **Carbon budgets of Central Appalachian forests with different harvest histories**



## ABSTRACT

Most scientists agree that regenerating forests contribute to the terrestrial carbon sink, but the potential carbon accumulation in response to forest harvest practices has been debated. The forests of the Central Appalachian Region have been regenerating over the past 100 years since the large-scale clear-cutting that occurred at the turn of the last century, but these forests have also been subject to a variety of management practices. This study compares the historical records of ecosystem carbon storage in four watersheds that have been harvested at different intervals and intensities since 1958. We compared NEP ( $\text{gC m}^{-2}\text{y}^{-1}$ ) and carbon balances in response to the four different harvest histories (no harvest, clear-cutting, single tree selection cutting, and 43cm diameter-limit cutting) using an ecosystem process model that was validated against dendrochronologic records. Harvest did not significantly impact average annual carbon sequestration, but the total carbon stored over a 55 year period was stimulated  $\sim 37\%$  with diameter-limit cutting and selective cutting. Average plant C ( $\text{g C m}^{-2}$ ) since 1950 was about 33% lower in response to a clear-cut event than plant C in an un-harvested forest, suggesting that the carbon accumulation associated with clear-cutting practices would decline over time and result in lower sequestration than diameter-limit cut, selective cut, or un-harvested forests. Depending on the fate of harvested wood, actual carbon sinks of forests are likely to be offset by carbon lost after wood products are consumed.

## INTRODUCTION

Land use changes pose one of the greatest human-induced impacts on ecological processes and have profound effects on the global terrestrial carbon budget. Vitousek *et al.* (1997) estimated that approximately 50% of land has been transformed by humans. Terrestrial carbon storage accounts for approximately 2300 Gt C (Denman *et al.* 2007) that is depleted by deforestation and harvest at a rate of about 2.55 Gt C/yr globally (Houghton 2003a). Thus, land transformations and forest management decisions may make a substantial contribution to changes in atmospheric carbon dioxide concentrations. There have been a number of attempts to quantify the effects of forest conversion on terrestrial carbon sinks (Houghton *et al.* 1999, Caspersen *et al.* 2000, Post and Kwon 2000, Pacala *et al.* 2001, Goodale *et al.* 2002, House *et al.* 2002), but the impacts of specific harvest strategies on ecosystem carbon storage is still uncertain.

Forest resources are continually challenged by societal and economic pressures (Turner *et al.* 1995). The value of forests in terms of carbon sequestration potential is often compromised by financial incentives to harvest wood products. Much of the Central Appalachian region consists of forested land that has regenerated following a major clear-cut event between 1880-1920 (Griffith and Widmann 2003). Most of this forest is privately owned and diverse economic principles and incentives in the region have led to a mosaic of forests with different harvest histories and economic values (Hicks 1998, Griffith and Widmann 2003, Parker *et al.* 2007).

This study examines the accumulation of carbon in central hardwood forests of the U.S. by estimating aboveground net primary productivity (ANPP) and net ecosystem productivity (NEP) of forested sites with different harvest histories. There is considerable debate about the relative carbon sequestration potential of forests in different age and disturbance classes. There are some studies that suggest that forest carbon uptake is increasing (Wofsy *et al.* 1993, Schimel *et al.* 2000), especially in temperate regions (Xiao *et al.* 1997, Houghton *et al.* 1999), but others

caution that the contribution of forest growth to terrestrial C sinks may be overestimated (Goodale *et al.* 2002, House *et al.* 2002, Beedlow *et al.* 2004). While most scientists agree that regenerating forests contribute to the terrestrial carbon sink, the potential C accumulation with future forest management practices has been debated and requires more detailed historical accounts of forest growth responses to harvest and environmental stimuli (Houghton 2003b). We compared historical records of forest carbon storage in four watersheds in the Fernow Experimental Forest (Parsons, WV) that have been harvested at different intervals and intensities since 1958. Our primary objective was to compare NEP and carbon balances in response to four different harvest histories (no harvest, clear-cutting, single tree selection cutting, and 43cm diameter-limit cutting) using an ecosystem model that was validated against dendrochronologic records. For this comparison, we used a modified version of an ecosystem productivity model, PnET-CN (Aber *et al.* 1997) that we previously validated for the nitrogen-saturated hardwood forests found in parts of West Virginia (PnET-CN<sub>sat</sub>, Chapter 2). This study provides a test of the versatility of PnET-CN<sub>sat</sub> by validating it against young regenerating forests after recent harvest events. Such application of this ecosystem productivity model is important for the Central Appalachians because harvest strategies often involve repeated cuts and result in an open canopy architecture. We further modified PnET-CN<sub>sat</sub> to account for this re-growth and forest development. Thus, a second objective was to test estimates of carbon sequestration that account for historical development of a harvested forest canopy in a region with high nitrogen availability.

## METHODS

### *Study sites*

This study was conducted in the Fernow Experimental Forest (FEF), a mixed mesophytic portion of the Appalachian Plateau (Braun 1950) where extensive logging took place between the years of 1903 and 1911 (Trimble 1977). The FEF has a fairly rainy and cool climate with an average maximum temperature of 15°C and about 122 cm of rainfall spread evenly throughout the year (USDA Forest Service, 2004). We chose four watersheds in the FEF that have had different harvest histories documented by the USDA Forest Service since the primary logging event ~100 years ago. Watershed 13 (WS 13) was subjected to very little disturbance since this logging period and is thus about 100 years old. Watershed 7 (WS 7) was clear-cut in several stages between 1963 and 1969 during which time forest re-growth was suppressed with herbicide treatments. Watershed 2 (WS 2) was subjected to diameter-limit cutting at different intervals between 1958 and the present (Table 1) with trees over 43 cm in diameter intermittently harvested about every 15 years. Watershed 5 (WS 5) underwent single tree selection cutting (selective cutting) with certain trees over 28 cm in diameter harvested periodically in a way that maintained a particular basal area and tree density as well as continued growth of trees in all age classes (more detailed description in Schuler 2004). Prior to these harvest events, we assumed that all watersheds were subject to similar disturbances. We estimated that 70% of biomass was removed in 1908 according to Forest Service records of clear-cut practices. About 95% mortality was estimated in response to logging but debris left behind to decompose constituted about 26% of the slashed organic matter, so about 70% of the total biomass was removed with 5% standing and 25% left behind). An equal account of the impact of chestnut blight was assigned to all watershed histories as well, which accounted for 25% biomass loss in the 1930s (Table 3.1). The percentage of biomass removed in each harvest event (Table 3.1) reflects the product of percent



Table 3.1. Timing of forest biomass removed due to harvest (the product of mortality and removal in PnET-CN<sub>sat</sub> harvest scenario) of experimental watersheds in the Fernow Experimental Forest. Column headings denote the harvest treatment (watershed number). The initial tree harvest was estimated from forest service records of logging practices in 1908 and it has been estimated that the Chestnut Blight and subsequent chestnut removal by loggers in the mid-1930's removed approximately 25% of the trees from these watersheds (Hicks 1998).

Year	Reference (WS 13)	Clear-cut (WS 7)	43cm diameter- limit (WS 2)	Single tree selection cut (WS 5)
1908	70%	70%	70%	70%
1935	25%	25%	25%	25%
1958			32%	21%
1963		49%		
1966		51%		
1968				15%
1969		98%		
1972			11%	
1978			5%	10%
1983				16%
1988			17%	14%
1996			17%	
1998				27%

mortality and the percent removed so that we are accounting for the residual debris that remained on the forest floor following disturbance.

#### *Dendrochronologic estimates of productivity and site-specific measurements*

Six circular 10m radius plots were randomly located and established in each of the four watersheds. We identified all of the trees in each plot to species, measured the diameter at breast height (DBH), and collected two increment cores from all trees >10cm DBH within each plot. We also cored all standing dead trees, though only a subset of these cores was suitable for further analysis. Tree increment cores were brought back to the lab where they were mounted and sanded with increasingly finer grades of sandpaper up to 2000 grit. With the exception of the cores from WS 7, all cores were crossdated using skeleton plots (Stokes and Smiley 1968) in order to assign biomass estimates to the appropriate year. Because WS 7 was clearcut in the 1960's, cores were too short to crossdate confidently. Following dating, ring widths of all watersheds were measured using a measuring stage and binocular microscope to determine annual growth increments to an accuracy of 0.01 mm. Crossdating was statistically confirmed using COFECHA (Grissino-Mayer 2001). For WS 7, species means of annual increment changes were dated according to the last year of growth, since crossdating was not an option.

Species-specific allometric equations (Tritton and Hornbeck 1982, Brenneman *et al.* 1978) were used to estimate woody biomass by compartment (equations do not include foliage) from stem diameters of living and dead trees. Estimates of annual wood production dating back to 1971 were calculated by subtracting the diameter increment of the subsequent year and applying the species-specific allometric equations. This approach results in increasing underestimates of productivity going back in time since fewer trees that died in prior years were included in our field measurements due to rot and decay. Some trees (~16%) were too rotten to either core or measure and, in these cases, a neighboring tree of the same species and similar size

( $\pm 10$ cm) was used as a substitute for that tree in plot level productivity calculations. One of the plots in WS 5 was not included in the aboveground productivity estimates because of errors made during field collections.

Litterfall collections, in combination with tree-ring data, were combined to estimate aboveground biomass and ANPP (Clark *et al.* 2001). Two litter baskets ( $0.23\text{m}^2$ ) located at random positions in each plot were sampled at monthly intervals for one year. Litter was sorted by species into leaf and woody litter, dried, and weighed. Litterfall mass measurements from WS 7 were also available from USDA Forest Service datasets for the years 1997-2001 (FERNOW Experimental Forest 2003). Foliar productivity estimates were added to annual wood productivity estimates to calculate ANPP in WS 7. We used the 5 year record from WS 7 to reconstruct ANPP over a historical 20 year period of ANPP measurements. Litterfall was also collected for one year in WS 13, WS 2, and WS 5 but we deemed this short dataset insufficient for estimating historical growth. In the case of WS2 and WS5, where stems were removed at repeated intervals, we estimated the proportional stem mass that would be represented by the harvested stems over time by adding the biomass removed at each harvest to the original dendrochronologic estimate, starting with the most recent. This was a coarse approximation of the actual biomass present between harvest intervals because it did not weigh individual species allometry results separately.

Site specific measurements of foliar [C] and [N] and litter [N] were made in the four watersheds. We collected foliar and litter samples for model validation in July of 2006. We sampled canopy leaves from dominant canopy tree species in each watershed ( $N = 120$ ). Leaf area of each leaf was measured within 5 hours of sampling and each leaf was dried for 48 hours ( $65^\circ\text{C}$ ) before being weighed. Dried samples were analyzed for carbon and nitrogen content by combustion in a Carlo Erba CN autoanalyzer (Fison Inst., Milan, Italy). Leaf mass per area (LMA) was also calculated for each leaf. Tree species sampled included *Acer rubrum*, *Acer*

*saccharum*, *Betula lenta*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Prunus serotina*, and *Quercus rubra*. At least five of these species were sampled in each watershed. Litter samples were also collected from six plots in each watershed. Three samples of litter were randomly collected from each plot and compiled. Carbon and nitrogen concentrations of dried litter samples were measured with the Carlo Erba CN autoanalyzer (Fison Inst., Milan, Italy). Stream flow records for each watershed were compiled from datasets maintained by the USDA Forest Service Northeastern Research Station (Fernow Experimental Forest 2003).

#### *Validation of PnET-CN<sub>sat</sub>*

An ecosystem productivity model, PnET-CN<sub>sat</sub> (Davis *et al. in review*), was parameterized for each watershed to more completely describe the effects of different harvest strategies on forest carbon balances, including net ecosystem productivity (NEP) and standing carbon pools. This model is a version of the PnET-CN model (Aber *et al.* 1997, Ollinger *et al.* 2002) that has been revised for the nitrogen-saturated forests that are found in the Central Appalachian Mountains and validated in a 100-year-old watershed (WS 13) in the FEF (Chapter 2). PnET-CN is a physiological process-based model that estimates productivity using carbon, nitrogen, and water budgets of a forest ecosystem and includes subroutines to describe the biomass removal associated with harvest or disturbance. Site specific parameters were described in Davis *et al. (in review)* and included AmaxA, AmaxB, SLWmax, GDDFolStart, GDDFolEnd, GDDWoodStart, GDDWoodEnd, FLPctN, WLPctN, MaxNStore, FolNRetrans, NReten, Nitr, Latitude, WHC, NRatio, SnowPack, and HON (defined in Table 3.2). Local climate files were constructed based on climate records from a weather station in the FEF that has been maintained by the USDA Forest Service Northeastern Research Station Timber and Watershed lab since 1952. Climate was reconstructed for the time period before 1952 using monthly averages of precipitation and temperature.

Table 3.2. Parameters specified according to on-site characteristics of the Fernow Experimental Forest. Parameters and definitions were all originally published in Aber et al. (1995, 1997)

Parameter	Definition
AmaxA	Intercept of the relationship between foliar N and saturated photosynthesis ( $A_{\max}$ )
AmaxB	Slope of the relationship between foliar N and saturated photosynthesis
FLPctN	Minimum N concentration in foliar litter
FoINCon	Concentration of foliar N
FoINRetrans	Proportion of foliar N that is retranslocated
GDDFolStart	Sum of all daily average temperature degrees above zero from Jan 1 to the start of foliage production
GDDFolEnd	Sum of all daily average temperature degrees above zero from Jan 1 to the end of foliage production
GDDWoodStart	Sum of all daily average temperature degrees above zero from Jan 1 to the start of foliage production
GDDWoodEnd	Sum of all daily average temperature degrees above zero from Jan 1 to the end of foliage production
HON	Proportion of N in humus organic matter
HalfSat	Light level at which photosynthesis is half saturated
K	Canopy light attenuation constant (a property of the leaves)
Lat	Latitude of site
MaxNStore	Maximum N in plant pool
Nitr	Nitrification rate
NReten	Proportion of N input retained in soil
NRatio	Mobile N as a percentage of maximum plant N
SLW <sub>max</sub>	Specific leaf weight at the top of the canopy (same as leaf mass per area)
SnowPack	Average depth of standing snow (0)
WHC	Water holding capacity: maximum amount of water that can be retained in soil
WLPctN	Minimum N concentration in woody litter

Despite our previous validation of PnET-CN<sub>sat</sub> in a mature forest (Chapter 2), the model structure is designed to reflect closed-canopy forests (Aber *et al.* 1992) and does not accurately predict the structure and productivity of young forests prior to canopy closure. In order to apply PnET-CN<sub>sat</sub> to regenerating forests, such as WS 7 that was clear-cut ~40 years ago, we modified the equation that allocates biomass to foliar growth. The new equation limits foliar growth to a percentage of the standing wood mass in any particular year so that a mature forest canopy is not assumed by the model until the wood mass is comparable to that of a mature forest (Yiqi Luo, personal communication). The percentage of foliar mass relative to wood mass was based on a comprehensive description of biomass pools in the FEF (Adams *et al.* 2004).

After parameterizing PnET-CN<sub>sat</sub> for the four watersheds, we tested the validation of the model against the dendrochronologic estimates of wood NPP, ANPP, historical records of stream flow, and on-site measurements of foliar [C], foliar [N], and woody litter [N]. We used regression analyses to determine the degree to which modeled estimates of wood NPP, ANPP, and stream flow predict measured values over time (SAS-JMP software version 5.1, SAS Institute, Cary, NC, USA). Annual comparisons of NPP were staggered by a year because the model assumed determinate bud growth and production lagged by one year compared to the dendrochronologic technique. We used a t-test (SAS-JMP software version 5.1, SAS Institute, Cary, NC, USA) to compare foliar C, foliar N, and woody litter N predictions to independent on-site measurements.

#### *Watershed carbon balance estimates*

With the validated PnET-CN<sub>sat</sub> model, we compared average carbon pools predicted in the four watersheds from 1958 to the present using a one-way ANOVA (SAS-JMP software version 5.1, SAS Institute, Cary, NC, USA). Model outputs that reflect ecosystem carbon pools included estimates of net ecosystem productivity (NEP), net carbon balance (NetCBal), and plant

carbon (PlantC). NEP was predicted on an annual basis ( $N = 46$ ) but NetCBal and PlantC were predicted on a monthly basis ( $N = 552$ ). Each of these estimates indicated carbon sequestration of the forested watersheds over time so we could examine the effects of harvests as they occurred starting in 1958. We also compiled annual averages of modeled GPP, NPP, NEP, autotrophic respiration, and heterotrophic respiration over the entire harvest treatment history (starting in 1958) and compared these averages to short-term averages of the same outputs over the period following the first harvest in each watershed (but before the second harvest). These long-term and short-term estimates provide two different perspectives of the effect of harvest on components in the ecosystem carbon budget.

## RESULTS

### *Validation of PnET-CN<sub>sat</sub> for four watersheds in the FEF*

In order to determine the accuracy of PnET-CN<sub>sat</sub> for predicting ecosystem carbon balances in Central Appalachian forests with different harvest histories, we validated the model by comparing modeled estimates of Wood NPP and streamflow to measurements in the four watersheds. In addition, we compared modeled estimates of woody litter [N], foliar [N] and foliar [C] to measurements in each watershed. In the case of ANPP, we used dendrochronologic estimates beginning in 1971 to include a timeframe for which the confidence in woody increment allometry for biomass remains high. Since we had litterfall estimates for multiple years only in the clear-cut watershed (WS 7), we compared modeled ANPP to measured ANPP for this watershed exclusively. The regression between measured and modeled estimates of ANPP was highly significant ( $r^2_{WS7} = 0.87, p < 0.0001$ ). We compared modeled wood NPP to measured wood NPP in all four watersheds. The regression of annual measured vs. annual modeled wood NPP estimates for all four watersheds was also significant ( $r^2_{WS13} = 0.11, p = 0.0714$ ;  $r^2_{WS7} =$

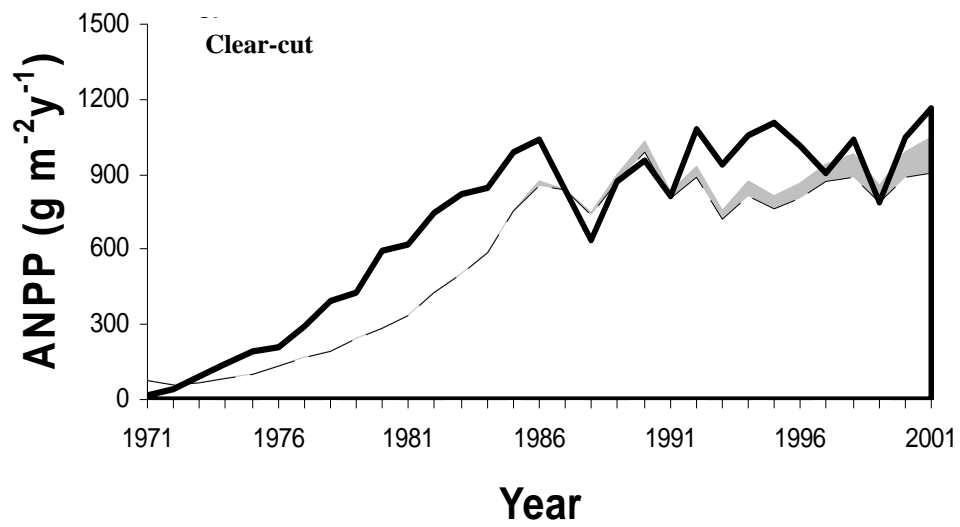


Figure 3.1. Aboveground net primary productivity (ANPP) of a forest clear-cut in the 1960s (WS7), calculated as the summation of litterfall data (as measured over 5 years) and annual woody increments. An estimate of ANPP with higher nitrogen retention is shown in gray for WS 7.



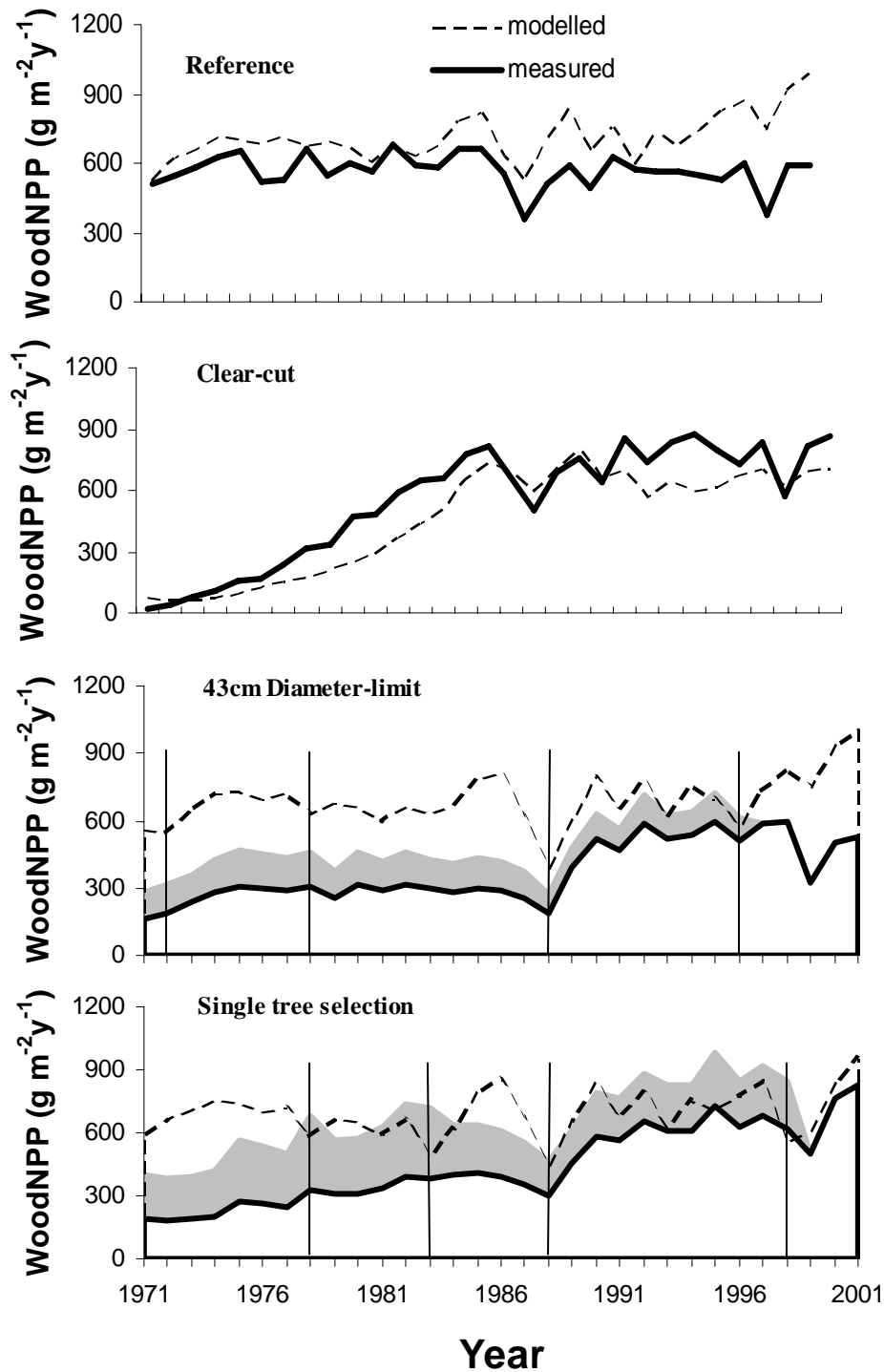


Figure 3.2. Twenty-year record of wood net primary productivity ( $\text{g m}^{-2} \text{y}^{-1}$ ) in each treatment watershed compared to modeled estimates for the same time period. All modeled estimates were generated with PnET-CN<sub>sat</sub> (Davis et al. in review). Vertical lines in the bottom two panels mark the years that correspond to diameter-limit cutting events. The accuracy of woody increment estimations declines in earlier years when representative stems would have been removed from the dendrochronologic samples. An estimate of wood productivity that includes wood that was removed during harvests is shown in gray.

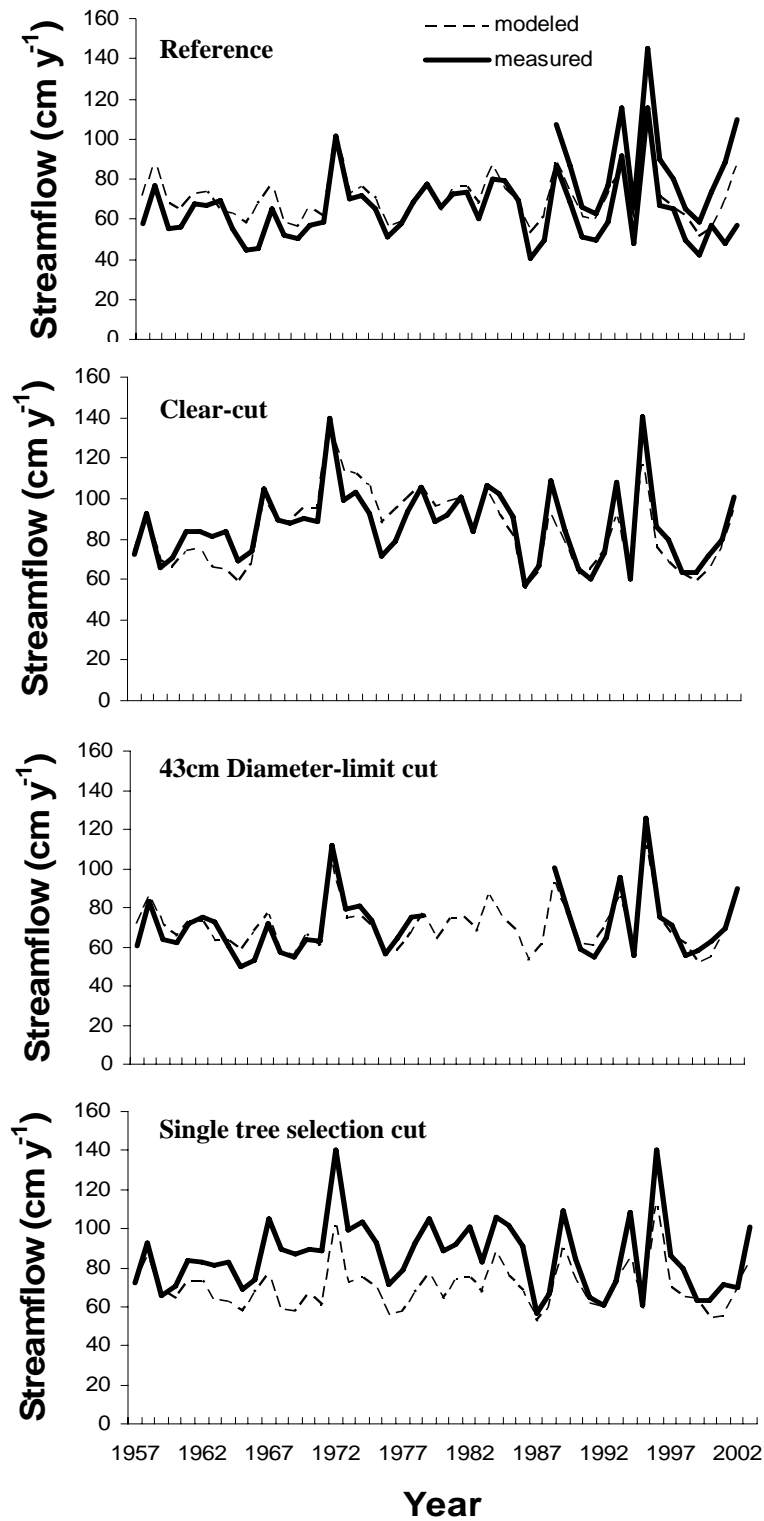


Figure 3.3. Historical record of streamflow measured since 1957 in the four experimental watersheds (WS13: un-harvested reference, WS7: clear-cut in 1960s, WS2: 48cm diameter-limit cut, WS5: single tree selection cut) by the USDA Forest Service Northeastern Research Station compared with modeled estimates from PnET-CN<sub>sat</sub>.

0.88,  $p < 0.0001$ ;  $r^2_{WS2} = 0.27$ ,  $p = 0.0029$ ;  $r^2_{WS5} = 0.18$ ,  $p = 0.0163$ ). The correlation of measured and modeled estimates for the clear-cut watershed (WS 7) was high indicating that the changes made to relative growth equations in the model were sufficient to reflect growth of a young regenerating forest. Modeled estimates of WS 7 ANPP and wood NPP (Figure 3.2) were around 5% and 12% lower than measured estimates during the 20 year period with dendrochronologic records (1971-2001). Model predictions of WS 13 productivity overestimated wood NPP by about 26% on average (Figure 3.2) over the 20 year period.

There was a clear disparity between the measured and modeled estimates of wood NPP in WS 2 and WS 5 in the years prior to 1990 (Figure 3.2). This divergence is a reflection of the trees that were removed during the diameter-limit and selective cuts that could not be included in the dendrochronology sampling. The back-calculated estimates of wood NPP that include removed (un-sampled) stem mass are visually represented by the shadow in figure 3.2. These back-calculations did not improve the overall correlation between modeled and measured wood NPP ( $r^2_{WS2} = 0.17$ ,  $p = 0.0219$ ;  $r^2_{WS5} = 0.10$ ,  $p = 0.0815$ ). Modeled wood NPP estimates were 54% and 5% higher than measured estimates in WS 2 and WS 5 respectively.

Stream flow measurements in each of the four watersheds were highly correlated with model predictions ( $r^2_{WS13} = 0.93$ ,  $p < 0.0001$ ;  $r^2_{WS4} = 0.77$ ,  $p < 0.0001$ ;  $r^2_{WS7} = 0.78$ ,  $p < 0.0001$ ;  $r^2_{WS2} = 0.87$ ,  $p < 0.0001$ ;  $r^2_{WS5} = 0.71$ ,  $p < 0.0001$ ). Modeled estimates were very similar to measured estimates over time; the only disparity was detected for estimates prior to 1985 in WS 5 (Figure 3.3). In WS 5 modeled estimates averaged 18% less than measurements. In contrast, modeled stream flow estimates were only 0.2% higher than measurements in WS 2 and 2.5% lower than measurements in WS 7. Streamflow predictions for the 100-year-old reference watersheds were 14% higher than measurements in WS 4 and 16% lower than measurements in WS 13.

Table 3.3. Comparison of modeled estimates (predicted) versus on-site measurements (observed) of nitrogen (N) and carbon (C) concentrations (%) in the four experimental watersheds at the Fernow Experimental Forest

	predicted	observed	<i>p</i>
Foliar [N]			
Reference	2.99	2.51	0.0328
Clear-cut	2.51	2.61	0.2551
Diameter-limit cut	3.03	2.36	<0.0001
Single tree selection cut	3.08	2.88	0.3952
Foliar [C]			
Reference	45.07	48.21	<0.0001
Clear-cut	45.14	48.73	<0.0001
Diameter-limit cut	45.14	48.16	<0.0001
Single tree selection cut	45.13	48.59	<0.0001
Wood litter [N]			
Reference	1.24	1.40	0.0974
Clear-cut	1.27	1.38	0.4642
Diameter-limit cut	1.29	1.03	0.0393
Single tree selection cut	1.29	1.13	0.1986

Modeled estimates of woody litter [N] were not significantly different from on-site measurements in WS 13, WS 7, and WS 5 (Table 3.3,  $p > 0.05$ ), but were significantly different than on-site measurements in WS 2 (Table 3.3,  $p = 0.0393$ ). Comparisons between modeled and measured foliar [N] and [C] showed mixed results. Average foliar [N] estimates over the last 5 years modeled were similar to on-site measurements in WS 5 and WS 7 ( $p > 0.05$ ) but model outputs of foliar [N] were significantly different from on-site estimates in WS 2 and WS 13 ( $p < 0.05$ ). Modeled predictions of foliar [C] during the last 5 years were significantly different than measurements made in all of the watersheds ( $p < 0.05$ ) despite the consistency of foliar [C] among watersheds (ranging from 48.2 to 48.7%). Modeled predictions of foliar [C] were consistently between 6.3 and 7.4% lower than on-site measurements.

#### *Forest carbon balance estimates*

After validating the PnET-CN<sub>sat</sub> model for the four forest watersheds, we examined carbon balances of each to predict the effect of the four different harvest histories on the carbon sequestration potential of Central Appalachian forests. Because of the high year-to-year variability, annual average NEP ( $\text{gC m}^{-2}\text{yr}^{-1}$ ) since 1958 was not significantly different among watersheds ( $F = 0.73$ ,  $p = 0.5381$ ). Averages by decade revealed a significant difference in NEP among harvest treatments in the 1970's when NEP of the clear-cut watershed (WS 7) was lower than that of the watersheds with diameter-limit cutting (WS 2), selective cutting (WS 5), and no harvest (WS 13) (interactive effect of harvest history and decade:  $F = 2.84$ ,  $p = 0.0006$ ). Total NEP of WS 7 since 1958 was about 12% higher than the total NEP of WS 13 (Figure 3.4). Both the diameter-limit and selection cut harvest watersheds had 37% higher total NEP than that estimated for WS 13. Average monthly carbon balance ( $\text{gC m}^{-2}$ ) (NetCBal) estimates were similar to NEP results, with no significant difference in the NetCBal among watersheds ( $F = 0.93$ ,  $p = 0.4275$ ). However, Plant C ( $\text{gC m}^{-2}$ ) estimates since 1958 were not similar among all

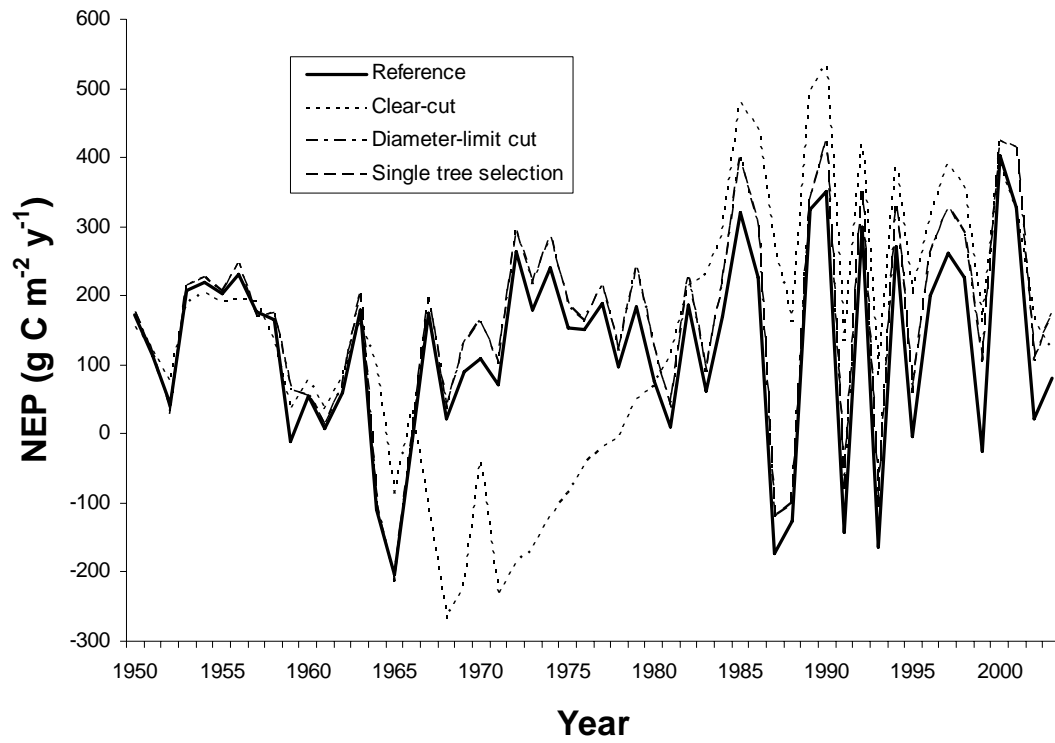


Figure 3.4. Modeled estimates (PnET-CN<sub>sat</sub>) of net ecosystem productivity (NEP) since 1950 in the four experimental watersheds (WS7: clear-cut in 1960s, WS13: un-harvested reference, WS2: 48cm diameter-limit cut, WS5: single tree selection cut).

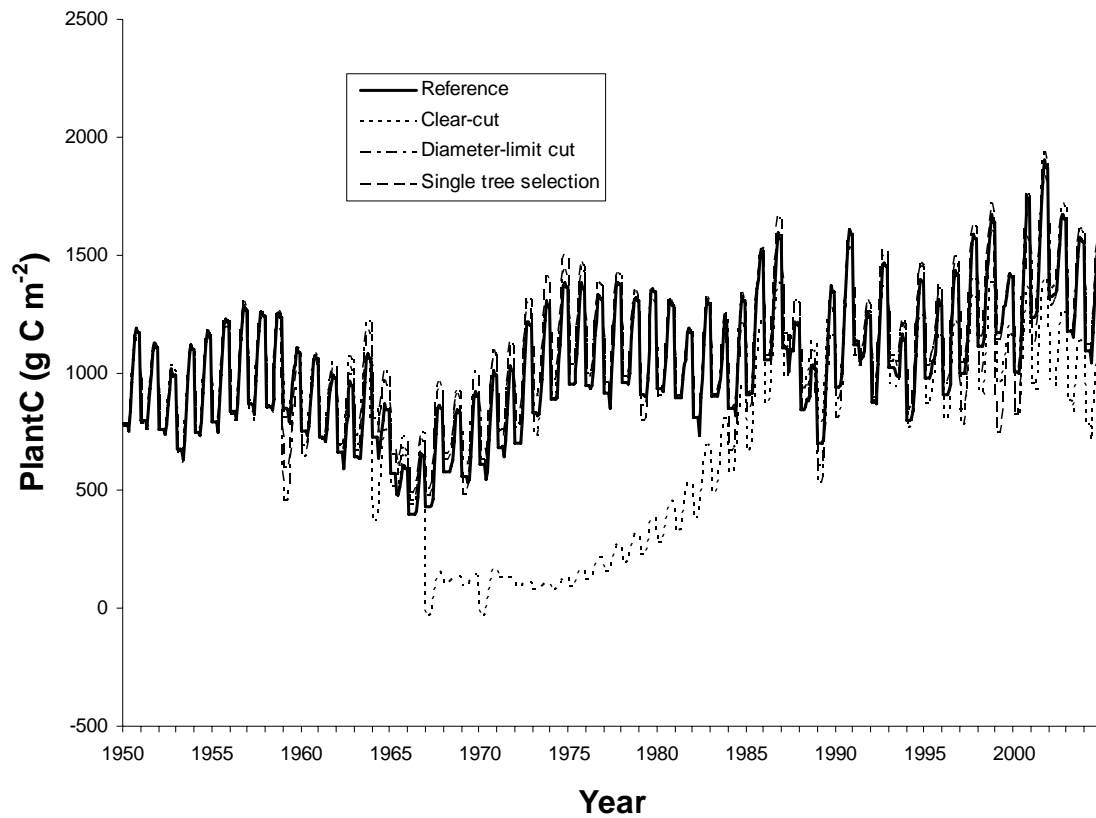


Figure 3.5. Modeled estimates ( $\text{PnET-CN}_{\text{sat}}$ ) of plant C (PlantC) since 1950 in the four experimental watersheds (WS7: clear-cut in 1960s, WS13: un-harvested reference, WS2: 48cm diameter-limit cut, WS5: single tree selection cut).

watersheds ( $F = 164.21$ ,  $p < 0.0001$ ). According to a post-hoc Tukey HSD test, average monthly plant C of the clear-cut watershed (WS 7) was significantly lower than the average plant C estimated in the other three watersheds ( $\alpha = 0.05$ ). Plant C in WS 7 was especially low in the 1970's following the clear-cut, but remained somewhat lower in the most recent decade as well (Figure 3.5). Average Plant C since 1958 was 33% lower in WS 7 than in the un-harvested watershed (WS 13), while modeled Plant C estimates for WS 2 and WS 5 were both about 1% higher than Plant C in WS 13.

The long-term carbon balances of the four watersheds were similar except in the case of the clear-cut watershed (Table 3.4). Gross primary productivity (GPP) of WS 7 was about 35% lower than GPP of the other three watersheds (ANOVA:  $F = 19.84$ ,  $p < 0.0001$ ; Tukey HSD:  $\alpha = 0.05$ ,  $Q = 2.5932$ ). Before the clear-cut event, GPP in WS 7 was only about 17% lower than the long-term average in the other watersheds, so clear-cutting appears to correspond to a 22% decline in GPP. The clear-cut harvest induced a similar decline in NPP as well as respiration, but declines in respiration were much higher so that the average post-harvest NEP of WS 7 was 138% higher than pre-harvest NEP and 51% higher than the long-term average NEP of WS13. The estimated carbon use efficiency (CUE) also increased after harvest by about 10% because of this respiration decline.

The diameter-limit cut and selective cut watersheds both showed stimulation in productivity over the long-term, including increases in GPP, NPP, and NEP. However, short-term productivity responses to harvest (in the years between the first and second harvest) were negative so that NEP in WS5 and WS2 was 70% and 45% lower than the control watershed NEP respectively (Table 3.4). Over time, the repeated recovery periods following each harvest eventually compensate for this initial reduction in productivity.



Table 3.4. Long-term (since 1958) and short-term carbon balances ( $\text{g C m}^{-2}\text{y}^{-1}$ ) of four watersheds subject to different harvest histories. Only long-term values are shown for the un-harvested watershed (WS13), pre- and post-harvest time periods were included for short-term estimates of carbon balances in the clear-cut watershed (WS7), and short-term estimates for the diameter-limit cut and single tree selection cut watersheds (WS2 and WS5) represent the years between the first and second harvest.

	Reference			Clear-cut			43cm Diameter-limit cut								Single tree selection cut									
	long-term			long-term			pre-harvest		post-harvest		long-term		Short-term		long-term		short-term							
GPP	733	±	177	478	±	270	619	±	33	484	±	285	745	±	172	609	±	130	754	±	177	589	±	151
TotalNPP	462	±	163	313	±	183	369	±	31	322	±	195	483	±	160	388	±	125	491	±	165	363	±	143
ANPP	377	±	72	241	±	147	342	±	24	246	±	153	371	±	74	292	±	45	369	±	74	292	±	46
CUE	0.61	±	0.10	0.64	±	0.15	0.60	±	0.03	0.66	±	0.16	0.63	±	0.10	0.62	±	0.11	0.63	±	0.10	0.59	±	0.13
Ra	271	±	33	165	±	100	249	±	18	161	±	104	262	±	35	221	±	20	263	±	35	226	±	27
Rh	347	±	29	185	±	72	296	±	12	149	±	42	326	±	24	326	±	34	334	±	21	332	±	28
NEP	115	±	150	128	±	208	73	±	40	174	±	211	157	±	152	63	±	114	157	±	157	32	±	132

## DISCUSSION

Land use history in the Central Appalachian Mountains can have a significant effect on short term carbon sequestration, but over longer periods of time the carbon storage capacity can average out to be similar in harvested and un-harvested forests. Despite this relative similarity in total NEP of the four experimental watersheds since 1958 (Figure 3.4), the decline in Plant C that was observed in WS 7 indicated that the carbon accumulation associated with clear-cut practices would decline with repeated application. In other words, if the wood productivity of a regenerated forest is lower following a clear-cut harvest than that of the original forest, then repeated harvests could have a deleterious effect on carbon storage over time. Seely *et al.* (2002) also observed a decline in plant C over time in response to repeated harvests of boreal tree species. This plant carbon decline was not evident following diameter-limit and selective cut harvests (Figure 3.5), suggesting that diameter-limit cutting may be a more sustainable way to stimulate carbon sequestration in managed forests.

Long-term trends in carbon budgets were especially important to consider in the case of diameter-limit cut and selective cut forests because repetitive harvests are likely to have cumulative effects on productivity over time. Short-term estimates of carbon pools after the initiation of these two harvest treatments were much lower than the long-term averages despite relatively similar respiration estimates. After the first harvest in each of these treatments, NEP estimates were 80% (WS 5) and 60% (WS 2) lower than long-term NEP with repeated harvests. This suggests that the interval at which these harvest treatments are applied can be an important determinant of carbon storage and productivity.

It is generally accepted that land use practices exert control over the accumulation of carbon in terrestrial ecosystems (Vitousek *et al.* 1997, Houghton *et al.* 1999, Caspersen *et al.* 2000, Pacala *et al.* 2001, Foster *et al.* 2003, Houghton, 2003a). The degree to which carbon accumulation is affected by wood harvest and forest regeneration is less certain due to the debate

over carbon budget changes with forest age and disturbance (Dixon et al. 1994). Following harvest events, the chronological changes in light regimes, nutrient dynamics, and metabolism impose cumulative regulation of carbon pools within a forest and can have long-lasting effects on the architecture and physiology of a forest ecosystem (Latty *et al.* 2004, Goodale and Aber 2001, and Yanai *et al.* 2003).

Our study simplified the estimation of carbon budgets in response to complex processes over time by relying on a validation tool that is chronological. Unfortunately, the living record of productivity in the diameter-limit and selective cutting treatments is incomplete due to the trees that were removed during harvests. Our approximation of the contribution the removed stems would make to productivity estimates (shadow in Figure 3.3) suggests that the model may be a more accurate reflection of actual productivity than the original dendrochronology estimates. Despite the error associated with earlier historical estimates, the PnET-CN<sub>sat</sub> model predicts measured wood productivity fairly well in recent years for these watersheds. Litter nitrogen estimates were also validated, but the inconsistency of foliar [N] predictions may be indicative of a light harvesting legacy that resulted with canopy openings that follow harvest. Latty *et al.* (2004) described the lasting effects that a period of high light can have on canopy physiology, and it is possible that acclimation of foliar N to light availability is stimulated for many years after high light conditions are present. Foliar N also tends to fluctuate from year to year such that the predictive power of the model for this output variable may increase with a longer-term dataset.

Changes in environmental conditions over time can induce temporal differences in ecosystem growth responses to harvest. For example, growth enhancement by atmospheric CO<sub>2</sub> is likely to be more profound for a young aggrading forest like WS7 in recent years than it was for the aggrading WS13 early in the last century (when atmospheric CO<sub>2</sub> was much lower). This effect should be reflected in the PnET-CN<sub>sat</sub> model estimates because we included a routine for

ramping CO<sub>2</sub> over time (Aber *et al.* 1995). Climate variability is an important driver of annual variability in ecosystem growth and nutrient pools. In some cases, productivity declined more in response to drought than in response to harvest events. For example, both measured and modeled productivity noticeably declined in all watersheds following the drought in 1988 and 1999 when precipitation was 13 and 15% lower than average respectively. The most severe drought period recorded in this region over the last century was in 1966 according to the Palmer Drought Severity Index (Palmer 1965, Dai *et al.* 2004), which also coincides with the clear-cutting event in WS7. The productivity response to this intense harvest would likely be more pronounced relative to the other watersheds if precipitation patterns were different during that time period.

There is some uncertainty about the physiological processes that drive productivity responses to climate change, land-use, and forest aging. For example, a conflict exists between evidence that respiration declines with growth rates over time (Pregitzer and Euskirchen 2004) and evidence that respiration increases with plant size (Reich *et al.* 2006). One might expect the foliar C results to be related to this debate because foliar C, derived as a proportion of plant C, could not be validated for any of the watersheds and reflects the overall plant carbon balance. The difference between measured and modeled foliar C estimates only ranged from 6.3 to 7.4% but the foliar C budget was not validated statistically because both predicted and observed carbon estimates were consistent (precise) within their respective datasets. If we scaled the ecosystem carbon budgets to account for the 6.3 to 7.4% inconsistency, the relative differences in carbon pools resulting from the four harvest scenarios would remain the same as our initial reports suggest.

The greatest uncertainty associated with our modeled results was likely due to variation in soil carbon with harvest events. Soil carbon has been challenging to quantify experimentally and thus presents a problem for model validation, but it is becoming more and more evident that soil plays an important role in ecosystem carbon budgets and land use change (Post and Kwon

2000, Guo and Gifford 2002, Rillig *et al.* 2003, Yanai *et al.* 2003, Beedlow *et al.* 2004). The high NEP predicted in WS7 after 1980 may be due to the soil carbon budget because the PlantC pool during this period is not higher than that of the other watersheds. Thus, the accumulation of carbon in the forest floor is likely to be high in this stage which is consistent with trends observed in other studies (Post and Kwon 2000, Guo and Gifford 2002, Yanai *et al.* 2003). In the model of biomass removal with harvest events we assumed that very little soil was removed from the system, but in reality there may have been substantial erosion associated with the clear-cut event. In the case of significant soil loss, our NEP estimates for WS7 would be inflated. Seely *et al.* (2002) found that soil carbon declined up to 20% in boreal spruce forests with frequent harvest rotations. Other studies have reported that harvest has no effect on the overall soil carbon budget (Johnson and Curtis 2001).

The end product of harvested wood must be considered in the final calculation of net carbon stored by a particular management practice. If harvested wood is converted to long standing wood products like furniture or structural materials then the wood removed is an additive contribution to carbon storage (C sink). On the other hand, wood that is burned, left on site to decompose, or converted to short-lived products (like paper that will soon decompose) represents a negative contribution to the carbon budget (C source). If forested ecosystems are to be managed for carbon accumulation, then these economic decisions must be considered in addition to ecosystem responses to harvest.

## CONCLUSION

Harvest does not significantly impact average annual carbon sequestration, but the total carbon sequestered over a 55 year period was stimulated ~37% by diameter-limit cutting and selective cutting. There may be some stimulation of carbon storage with clear-cutting practices as well, but the carbon gains are not sustainable and are likely to be offset by subtracting carbon lost after wood products are consumed. Thus, in the case of the harvest scenarios investigated

here, actual net carbon sequestered depends more on the fate of the wood products removed during harvest than the harvest technique.

#### ACKNOWLEDGEMENTS

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## Chapter 4

### **Foliar nitrogen concentrations measured along an elevation gradient at two spatial scales in Central Appalachian forests**



## ABSTRACT

Regional topography and climate variation yield differences in ecosystem attributes that make spatially scaled estimates of forest productivity challenging. Foliar nitrogen is a primary indicator of forest ecosystem productivity and is used in regional estimates of terrestrial productivity, but this characteristic has not been well described in the Central Appalachian region. Here we describe foliar and soil N variation among species and elevations at two spatial scales in the Central Appalachian region: (1) across the Elklick watershed in the Fernow Experimental Forest and (2) across the state of West Virginia. We found higher foliar N concentrations at both scales than those previously reported and applied to regional models of productivity. Effects of elevation on foliar and soil nutrient status were more evident in the Fernow than generally observed across WV. Soil N concentrations in the Fernow were two times greater than those observed across West Virginia. Species related differences were observed at both spatial scales, but were not always consistent. Canopy foliar N ranges may be consistent across elevations throughout the state of WV, but should be scaled according to species-related elevation effects for studies that estimate productivity differences in response to changing species composition.

## INTRODUCTION

Structure and function of forest ecosystems differ with topography, latitude, and climate patterns. The resulting spatial variation presents a challenge for estimating regional and global terrestrial productivity (Houghton 2003). Foliar properties that are highly correlated with carbon assimilation and productivity differ across forested biomes of the world (Reich *et al.* 1999a, Wright *et al.* 2004), as well as across terrain within a biome (Turner *et al.* 2000, Luo *et al.* 2005). Spatial variation of anthropogenic influences adds another dimension of complexity to forest ecosystem characteristics because the intensity of land use and concentrations of atmospheric pollutants are not consistent over space and time.

The need for regional forest productivity assessments has fostered large-scaled estimations based on generalized ecosystem attributes that are applied across broad landscapes. Foliar N concentrations are important indicators of forest growth and are widely used in ecosystem models of productivity (Running and Gower 1991, Aber and Federer 1992, Landsberg and Waring 1997). Thus, it is essential to characterize spatial variation of foliar N before accurate estimates of terrestrial carbon sequestration can be made. Remote sensing is often used to estimate foliar N across a landscape, but this technique provides very little information about canopy structure and no information about the forest floor or understory vegetation that are important components of ecosystem nutrient cycling (Pastor *et al.* 1984, Reich *et al.* 1997). Studies that compare productivity estimates derived from foliar N measurements at varied spatial resolutions have concluded that substantial error can be introduced by ignoring small scale N variation (Reich *et al.* 1999b, Pan *et al.* 2004) and, thus, remotely sensed forest N characterizations may not be detailed enough for accurate productivity estimates across a heterogeneous landscape.

Regional estimates of forest productivity in the Central Appalachian Mountains are often based on foliar N measurements made in the New England or the Southern Appalachian regions

(McNulty *et al.* 1994, Smith *et al.* 2002, Pan *et al.* 2004, Hom *et al.* 2006). In addition, most of the foliar N measurements that are used to parameterize productivity models in the Central Appalachian region were made in N-limited ecosystems (Field and Mooney 1986, Reich *et al.* 1992). Over the past 50 years, the Central Appalachian Mountains have been subjected to higher concentrations of N deposition than many New England and Southern Appalachian sites that have extensive foliar N datasets (Ollinger *et al.* 1993, US EPA 2002, US EPA 2006). The Fernow Experimental Forest (Parsons, WV) in the Central Appalachian Mountains is positioned in a location with high historical rates of N deposition and shows signs of N saturation (Peterjohn *et al.* 1996, Gilliam *et al.* 2001, US EPA 2002). Nitrogen-saturated sites are becoming more common, but this nutrient status is not characteristic of the mixed deciduous forests of the eastern United States. Thus, there may be a range of foliar and soil N concentrations in West Virginia that extends outside the range of observations in other eastern U.S. forests (Nadelhoffer *et al.* 1999, Lovett *et al.* 2002).

Nitrogen deposition and other environmental factors, such as temperature and precipitation, in mountainous regions are likely to vary with elevation (Ollinger *et al.* 1993) even at a small scale. Some studies have documented that foliar N increases with elevation, but these studies included only a few representative tree species from a particular forest ecosystem (Aber *et al.* 2003, Ollinger and Smith 2005, Luo *et al.* 2005). Aber *et al.* (2003) documented foliar N of sugar maple trees across an elevation gradient by pooling data from several study sites in the northeastern United States, but included only two sites in the Central Appalachian Mountains that were located substantially south of the other 157 sites. The degree of variation in foliar N with elevation may differ across latitudes and has been given very little attention in the Central Appalachian region.

West Virginia is a heavily forested state and it comprises a substantial component of the mature forest land in the Central Appalachian Mountains. The high diversity of tree species and

the significant elevation range (200 to 1400 meters) in West Virginia provides a model for examining the interactive effects of species and elevation on foliar N in the Central Appalachian Mountains. The objective of our study was to compare the effects of species and elevation on foliar N concentrations of temperate deciduous forest canopies at two spatial scales, the watershed scale and the statewide scale. We investigated foliar N variation across a range of elevations in a mature forested watershed in the Fernow Experimental Forest and compared these trends to measurements made across the larger range of elevations throughout the state of WV. In particular we were interested in whether leaf N at the top of the forest canopy varies with elevation and species at both spatial scales, whether variations in soil N also exist along the same elevation gradient, and whether the effect of elevation is consistent between the two spatial scales.

## METHODS

### *“Small-scale” watershed study*

The small-scale component of this study was conducted in the Fernow Experimental Forest (Fernow), a 1900 hectare subsection of the Monongahela National Forest near Parsons, WV. The Fernow is within the Appalachian Plateau of the central hardwood region and is classified as mixed mesophytic according to Braun (1950). This region was extensively logged between 1903 and 1911 (Trimble 1977) and has been owned by the U.S. Forest Service since 1915 (Schuler 2004). Research and forest monitoring efforts were initiated in 1933 (Schuler 2004) but portions of the forest have regenerated naturally over the past 100 years. The climate that accompanied this regeneration period was moist and cool with an average maximum temperature of 15°C and about 122 cm of rainfall spread evenly throughout the year (U.S.D.A Forest Service, 2004).



We established three transects southeast of Elklick Run that traverse relatively unmanaged sections of the Fernow (Adams, personal communication) and sampled 30 m radius circular plots at three elevations ranging from 550 to 1090 m (1800 to 3650 ft). Similar slope and aspect were maintained along each transect in order to minimize the variation that may occur as a result of topographic differences other than elevation (Fekedulegn *et al.* 2002). At least five species of dominant canopy trees were identified and marked for sampling in each plot. The species sampled included *Acer saccharum*, *Betula lenta*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Prunus serotina*, and *Quercus rubra*. A 12-gauge semi-automatic shotgun was used to collect small twigs with canopy leaves attached from the tree tops. Each leaf sample was cut into 2.3 cm<sup>2</sup> disks, dried for 48 h at 65°C, and weighed so that leaf mass per unit area (LMA, g·m<sup>-2</sup>) could be calculated. Carbon and N content of all dried leaf samples were analyzed with a Carlo Erba CN autoanalyzer (Fison Inst., Milan, Italy).

Soil samples were collected from the A horizon at three locations within 2 m of the base of each canopy tree sampled using a 1.9 cm diameter soil corer. The depth of each core was recorded to estimate sample volume. All three soil samples for each individual tree were consolidated, dried for 48 h at 65°C and weighed. Bulk density was calculated as the mass of soil in a given volume. The carbon and N content of dried soil samples were analyzed using Dumas combustion in a Carlo Erba CN autoanalyzer (Fisons Instr., Milan, Italy).

#### *“Large-scale” statewide study*

The large-scale portion of this study was conducted by sampling four “mega-transects” that traverse a range of elevations (~200 to 1400 m) found in the state of West Virginia. All of the mega-transects run east to west across the state with an average distance between sites of 80 km. All sites were mature, closed-canopy deciduous forests with canopy trees at least 30 cm in diameter at breast height. The top ten most abundant canopy trees in the state were identified

from U.S. Forest Service records and canopy foliage from the tops of trees was collected from at least five of these dominant canopy species at each sampling site using a 12-gauge semi-automatic shotgun. The species sampled included *Acer rubrum*, *Acer saccharum*, *Betula lenta*, *Carya* spp., *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Prunus serotina*, *Quercus alba*, *Quercus rubra*, and *Tilia americana*. Leaf disks were cut, dried for 48 hours at 65°C, and weighed so that LMA could be calculated.

Soil samples were collected from the A horizon at four locations within 2 m of the base of each tree using a 1.9 cm diameter soil corer. The four soil samples from each tree location were combined, dried for 48 hours at 65°C and weighed. Bulk density of the soil was calculated as the mass per volume of soil. All dried soil and leaf tissue samples were analyzed using Dumas combustion in a Carlo Erba CN autoanalyzer (Fisons Instr., Milan, Italy) to measure carbon and N content.

### *Data Analysis*

Many of the species sampled in the Fernow watershed were also sampled at sites across the state but there was not complete overlap of all species at both spatial scales. Thus, we examined datasets from the watershed and statewide scales separately for interactive and main effects of elevation and species on leaf and soil characteristics using a 2-way ANCOVA (SAS-JMP software) with elevation as the covariate. If significant differences were detected, then analysis of variation among treatment groups was further assessed with Tukey-Kramer HSD tests.

In order to test the spatial variation of ecosystem scaled N concentrations, we conducted a test of the consistency of N changes with elevation at the two spatial scales. Since we were interested in spatial variation of generalized ecosystem traits, we lumped all species together for this analysis. We tested the consistency of foliar and soil nitrogen trends with elevation between

the statewide and watershed scales using a 2-way ANCOVA with spatial scale as a main effect and elevation as a covariate (SAS-JMP software).

## RESULTS

### *Species and elevation effects at the watershed scale (Elklick watershed)*

In the Elklick watershed of the Fernow, there was no significant effect of elevation on foliar  $N_{\text{mass}}$  ( $F_{\text{elev}} = 1.3238$ ,  $p_{\text{elev}} = 0.2555$ ), but foliar  $N_{\text{area}}$  increased with elevation ( $F_{\text{elev}} = 9.1596$ ,  $p_{\text{elev}} = 0.0040$ ) (Figure 4.1). This change was paralleled by increases in soil C:N (Table 4.1) and was similar among species ( $F_{\text{spp} \times \text{elev}} = 0.4395$ ,  $p = 0.8186$ ). Despite this similarity in species responses to elevation, there were differences in mean foliar N concentrations among species (Figure 4.2;  $N_{\text{area}}$ :  $F_{\text{spp}} = 4.8756$ ,  $p_{\text{spp}} = 0.0012$ ;  $N_{\text{mass}}$ :  $F_{\text{spp}} = 9.3863$ ,  $p_{\text{spp}} < 0.0001$ ).

*Prunus serotina* foliage had the highest overall  $N_{\text{area}}$ , almost 100% greater than that observed in the *Fagus grandifolia* leaves. *Fagus grandifolia* leaves also had the lowest LMA of all species sampled in the Fernow, although not significantly less than *Prunus serotina*. *Quercus rubra* had the thickest leaves with 83% greater LMA than that of *Fagus grandifolia* leaves. In addition to the effect of species on LMA ( $F_{\text{spp}} = 4.6363$ ,  $p = 0.0016$ ), there was also an elevation effect on LMA ( $F_{\text{elev}} = 7.4779$ ,  $p = 0.0088$ ) that was similar for all species ( $F_{\text{spp} \times \text{elev}} = 0.5575$ ,  $p = 0.7318$ ). Variation in  $N_{\text{mass}}$  due to species was more modest (Figure 4.2;  $F_{\text{spp}} = 9.3863$ ,  $p < 0.0001$ ) than species effects on LMA and  $N_{\text{area}}$ . *Acer saccharum* leaves had the lowest  $N_{\text{mass}}$  and *Liriodendron tulipifera* leaves had the highest  $N_{\text{mass}}$  (32% greater than *A. saccharum*).

There were significant changes in soil C:N ratios and bulk density with elevation in the Fernow (Table 4.1). Soil C:N increased with elevation ( $F_{\text{elev}} = 56.1265$ ,  $p_{\text{elev}} < 0.0001$ ) and bulk density decreased with elevation ( $F_{\text{elev}} = 5.4708$ ,  $p_{\text{elev}} = 0.0213$ ). There were no significant effects of tree species on any of the soil variables but the bulk density change with elevation was

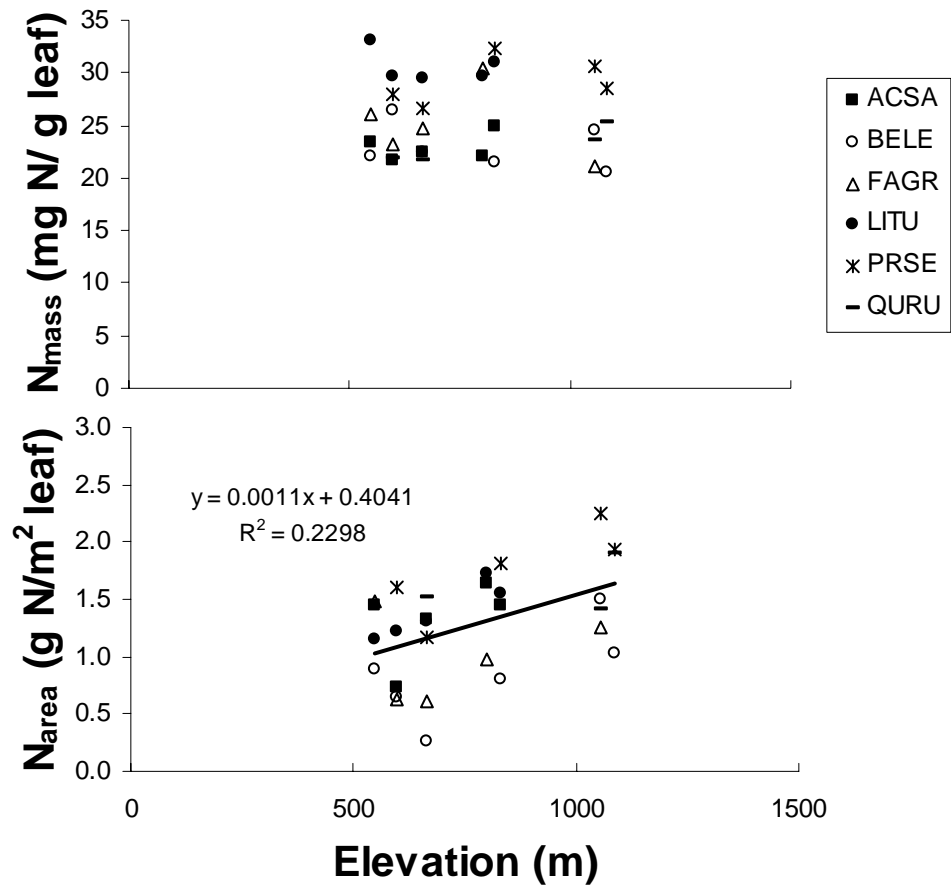


Figure 4.1. Comparison of trends in mass based foliar [N] ( $N_{\text{mass}}$ , top panel) and area based foliar [N] ( $N_{\text{area}}$ , bottom panel) in the Fernow Experimental Forest (Fernow). Each data point represents a plot mean for a tree species including *Acer saccharum* (ACSA), *Betula lenta* (BELE), *Fagus grandifolia* (FAGR), *Liriodendron tulipifera* (LITU), *Prunus serotina* (PRSE), and *Quercus rubra* (QURU). A line is fitted to show the relationship of  $N_{\text{area}}$  to elevation.

Table 4.1. Soil properties of samples collected at two spatial scales.

Study site	Tree species	n	soil %N <sup>+</sup>			soil %C <sup>+</sup>			soil C:N			bulk density		
			mean	std. err.		mean	std. err.		mean	std. err.		mean	std. err.	
Fernow	<i>Acer saccharum</i>	29	0.540	0.036		5.426	0.580	*	10.280	0.768	*	0.548	0.036	
Fernow	<i>Betula lenta</i>	18	0.480	0.024		5.302	0.533	*	11.154	1.144	*	0.722	0.064	
Fernow	<i>Fagus grandifolia</i>	25	0.505	0.032		4.960	0.548	*	10.178	0.847	*	0.583	0.045	
Fernow	<i>Liriodendron tulipifera</i>	20	0.490	0.032		4.261	0.455		8.523	0.513	*	0.652	0.049	
Fernow	<i>Prunus serotina</i>	18	0.571	0.049		6.464	1.055	*	11.070	1.167	*	0.597	0.054	
Fernow	<i>Quercus rubra</i>	17	0.564	0.057	*	8.279	1.362	*	14.009	1.416	*	0.532	0.069	**
West Virginia	<i>Acer rubrum</i>	23	0.273	0.029		4.522	0.556		15.97	0.6686		1.039	0.113	
West Virginia	<i>Acer saccharum</i>	23	0.270	0.031	*	4.043	0.467	*	14.91	0.472		1.039	0.062	
West Virginia	<i>Carya spp.</i>	34	0.247	0.028	*	3.385	0.313	*	14.95	0.4009		1.059	0.075	
West Virginia	<i>Fagus grandifolia</i>	21	0.219	0.023	*	4.053	0.493	*	18.31	0.6293		0.967	0.041	
West Virginia	<i>Fraxinus americana</i>	7	0.242	0.042		3.313	0.660		13.4	0.7038		1.357	0.141	
West Virginia	<i>Liriodendron tulipifera</i>	33	0.279	0.021		4.541	0.483		15.85	0.6897		1.067	0.076	
West Virginia	<i>Prunus serotina</i>	19	0.322	0.059	*	4.268	0.527		15.69	0.7938		0.982	0.053	
West Virginia	<i>Quercus alba</i>	31	0.262	0.028		4.517	0.515		17.14	0.8041		0.957	0.051	
West Virginia	<i>Quercus rubra</i>	38	0.264	0.032		4.391	0.489		17.87	0.8299		1.114	0.052	
West Virginia	<i>Tilia americana</i>	11	0.292	0.029		4.142	0.447		14.31	0.9846		0.850	0.060	

\* linear regression on elevation is significant ( $\alpha = 0.05$ ) and the relationship is positive

\*\* linear regression on elevation is significant ( $\alpha = 0.05$ ) and the relationship is negative

<sup>+</sup> For samples collected in West Virginia data were log transformed prior to statistical analysis to attain normal distribution. Means shown represent the original dataset.

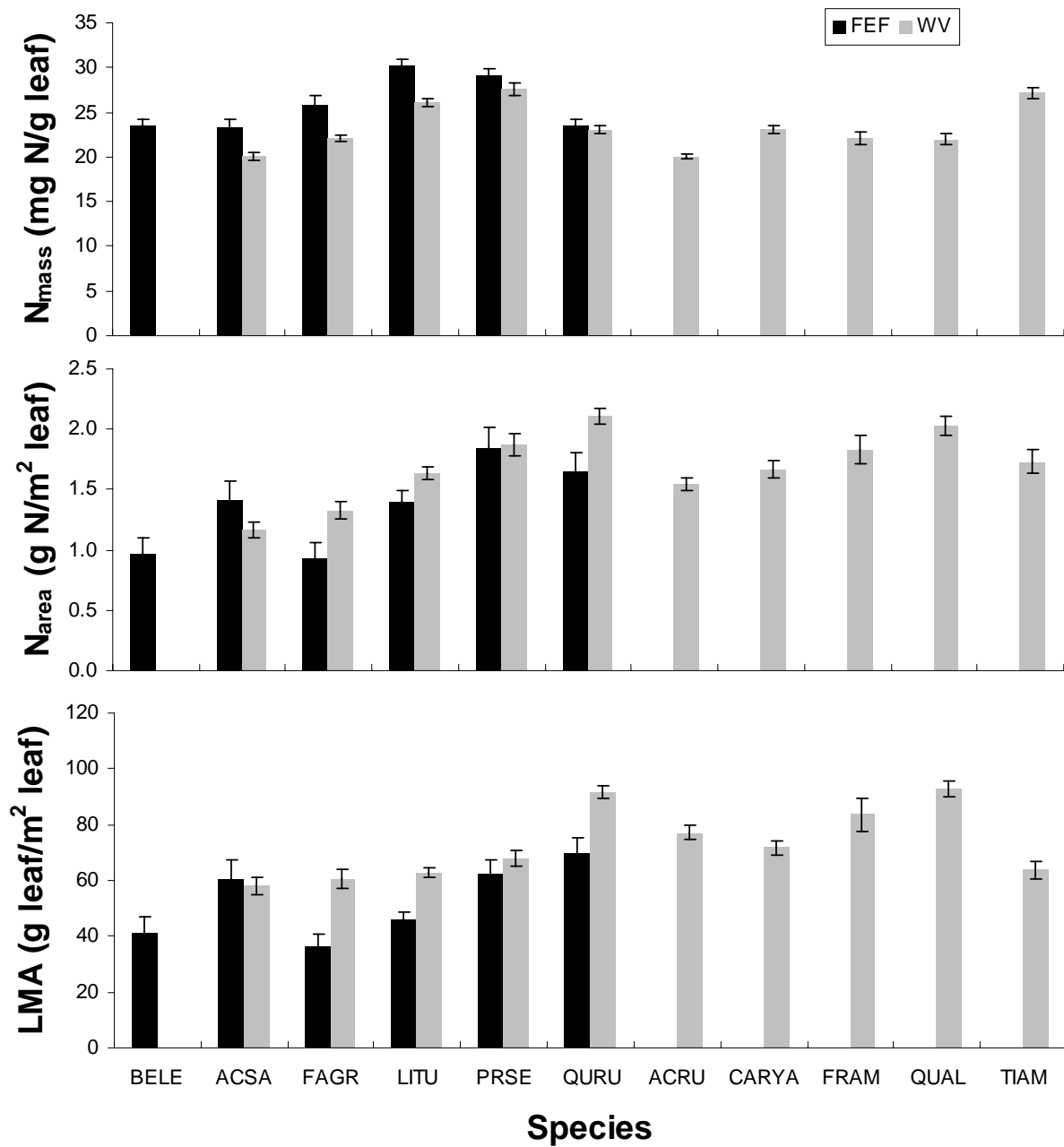


Figure 4.2. Foliar [N] on a mass basis ( $N_{\text{mass}}$ ), foliar [N] on an area basis ( $N_{\text{area}}$ ), and leaf mass per area (LMA) of eleven hardwood tree species (BELE: *Betula lenta*, ACSA: *Acer saccharum*, FAGR: *Fagus grandifolia*, LITU: *Liriodendron tulipifera*, PRSE: *Prunus serotina*, QURU: *Quercus rubra*, ACRU: *Acer rubrum*, CARYA: *Carya* spp., FRAM: *Fraxinus americana*, QUAL: *Quercus alba*, TIAM: *Tilia Americana*) in the Fernow Experimental Forest (FEF) in black and across West Virginia (WV) in gray. Error bars represent standard error.

driven mostly by the differences observed in soils associated with *Quercus rubra* trees (Table 4.1;  $R^2 = 0.72$ ,  $p = 0.0002$ ).

#### *Species and elevation effects at a statewide scale (West Virginia)*

At the statewide scale, the effects of elevation on both  $N_{\text{area}}$  and  $N_{\text{mass}}$  differed by species (Figure 4.3;  $N_{\text{area}}$ :  $F_{\text{elev} \times \text{spp}} = 2.2297$ ,  $p_{\text{elev} \times \text{spp}} = 0.0203$ ;  $N_{\text{mass}}$ :  $F_{\text{elev} \times \text{spp}} = 5.2415$ ,  $p_{\text{elev} \times \text{spp}} < 0.0001$ ). For five species across the state, a portion of the  $N_{\text{mass}}$  variation was explained by elevation (Figure 4.4). Foliar  $N_{\text{mass}}$  of *Quercus alba* was affected the most across the statewide elevation gradient, increasing 65% over 655 m in altitude ( $R^2 = 0.4383$ ). In contrast,  $N_{\text{mass}}$  of *A. saccharum* leaves was affected by elevation but increased by only 16% over an 1100 m elevation change. Among the ten species sampled across WV, those with the highest correlation between  $N_{\text{area}}$  and elevation were *Acer rubrum*, *Acer saccharum*, and *Quercus alba* (Figure 4.4). The change in LMA with elevation also differed by species ( $F_{\text{elev} \times \text{spp}} = 2.3261$ ,  $p = 0.0153$ ). LMA of *Acer rubrum* responded most to elevation, paralleling the change in  $N_{\text{area}}$ , but LMA of *Carya* spp. declined with elevation and the other species showed very little response.

Changes in soil quality with elevation were less apparent at the statewide scale than those observed in the Fernow watershed (Table 4.1). There were significant increases in the percentage of soil C and soil N along the state elevation gradient (%C:  $F_{\text{elev}} = 18.62$ ,  $p_{\text{elev}} < 0.0001$ ; %N:  $F_{\text{elev}} = 17.03$ ,  $p_{\text{elev}} < 0.0001$ ) and no difference in this effect nor overall mean soil C and N was observed among species (%C:  $F_{\text{spp}} = 1.2047$ ,  $p_{\text{spp}} = 0.2933$ ; %N:  $F_{\text{spp}} = 1.1233$ ,  $p_{\text{spp}} = 0.3472$ ). These increases in C and N were proportional such that C:N was not affected by elevation (Table 4.1). There were, however, differences in C:N ratios among soils associated with different species ( $F_{\text{spp}} = 3.7108$ ,  $p_{\text{spp}} = 0.0002$ ). Soils surrounding *Fagus grandifolia* and *Quercus rubra* trees had significantly higher C:N ratios than soils around *Carya* spp. and *Acer saccharum* trees according to a Tukey HSD test ( $\alpha = 0.05$ , Table 4.1). No differences in soil bulk density were observed among species or elevation ( $p > 0.05$ ).

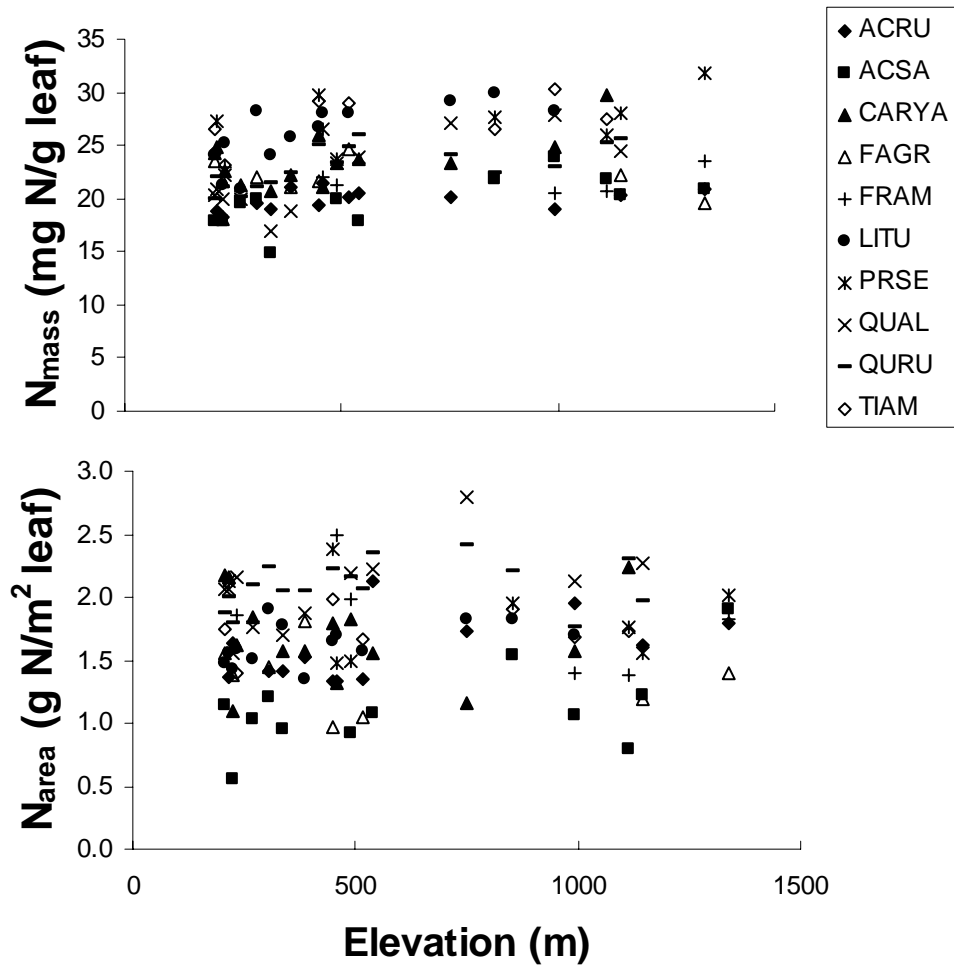


Figure 4.3. Mass based foliar [N] ( $N_{\text{mass}}$ , top panel) and area based foliar [N] ( $N_{\text{area}}$ , bottom panel) in West Virginia (WV). Each data point represents a plot mean for a tree species (BELE: *Betula lenta*, ACRU: *Acer rubrum*, ACSA: *Acer saccharum*, CARYA: *Carya* spp., FAGR: *Fagus grandifolia*, FRAM: *Fraxinus americana*, LITU: *Liriodendron tulipifera*, PRSE: *Prunus serotina*, QUAL: *Quercus alba*, QURU: *Quercus rubra*, TIAM: *Tilia americana*).



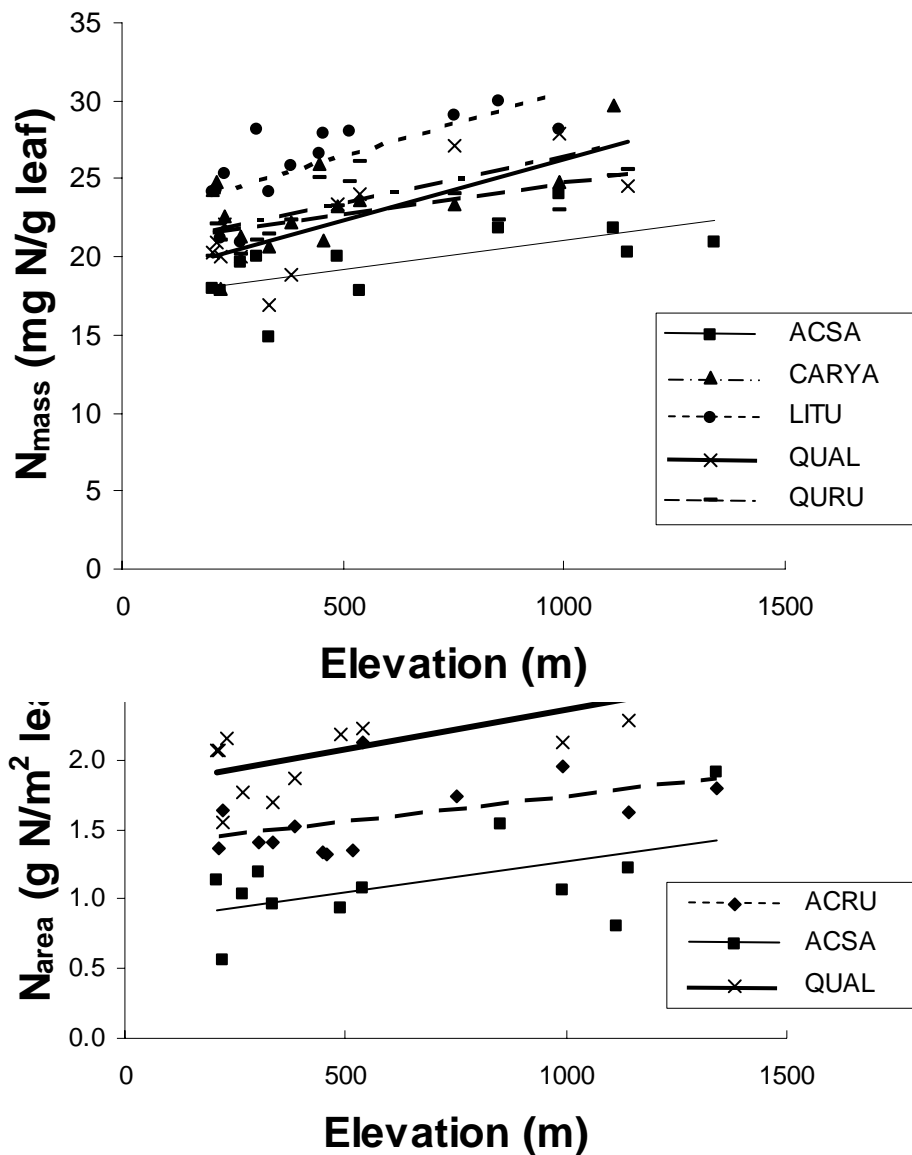


Figure 4.4. Foliar [N] on an area basis ( $N_{area}$ ) and mass basis ( $N_{mass}$ ) of canopy leaves from hardwood species growing along an elevation gradient in West Virginia. Of the total species sampled, only those species with foliar N that is correlated with elevation [species x elevation effect on  $N_{mass}$ :  $F = 5.2415$ ,  $p < 0.0001$ ; species x elevation effect on  $N_{area}$ :  $F = 2.2297$ ,  $p = 0.0203$ ; species x elevation effect on LMA:  $F = 2.3261$ ,  $p = 0.0153$ ] (ACSA: *Acer saccharum*, ACRU: *Acer rubrum*, CARYA: *Carya* spp., LITU: *Liriodendron tulipifera*, QUAL: *Quercus alba*, QURU: *Quercus rubra*).  $N_{area}$  was log transformed and LMA was square root transformed for normal distribution, but data shown are true plot means.

### *Foliar N at two spatial scales*

Terrestrial carbon sequestration associated with forest productivity is often estimated for whole ecosystems without assessing individual species contributions or community composition. In these cases it is important to understand the degree to which ecosystem traits are conserved as the geographic area of interest increases from a watershed scale to a larger regional scale. Our final analysis addressed this issue by comparing the elevation trends observed at the watershed scale and the state scale.

The effect of elevation on  $N_{\text{area}}$  of the forest canopy varied at the two spatial scales ( $F_{\text{scale} \times \text{elev}} = 17.3397, p < 0.0001$ ). In the Fernow,  $N_{\text{area}}$  increased with elevation but this change was not observed across WV (Figure 4.5). Similarly, LMA increased with elevation in the Fernow but not across WV ( $F_{\text{scale} \times \text{elev}} = 23.0566, p < 0.0001$ ) (Figure 4.5). The weight-based C and N concentrations of forest canopy leaves were significantly different between the two spatial scales (%C:  $F_{\text{scale}} = 158.12, p < 0.0001$ ;  $N_{\text{mass}}$ :  $F_{\text{scale}} = 14.408, p = 0.0002$ ) with no effect of elevation observed on these two variables. The mean percentage of C observed in the Fernow was 7% greater than leaf C measured across the state of WV. Mean  $N_{\text{mass}}$  was 12% greater in the Fernow than the statewide mean (Figure 4.2).

The magnitude of change in soil N with elevation was similar at both spatial scales ( $F_{\text{elev}} = 6.69, p = 0.0101$ ) but the mean soil N in the Fernow was 97% greater than the mean soil  $N_{\text{mass}}$  across WV ( $F_{\text{scale}} = 125.31, p < 0.0001$ ). Soil C concentrations did not respond to elevation in the same manner at the two spatial scales ( $F_{\text{scale} \times \text{elev}} = 25.78, p < 0.0001$ ). Soil  $C_{\text{mass}}$  increased more dramatically with elevation in the Fernow than across the state such that soil C:N changed with elevation in the Fernow, but not across the WV elevation gradient ( $F_{\text{scale} \times \text{elev}} = 65.48, p < 0.0001$ ). The difference between the two spatial scales was also evident in bulk density observations because bulk density decreased with elevation in the Fernow while remaining relatively constant across elevations throughout the state of WV ( $F_{\text{scale} \times \text{elev}} = 6.05, p = 0.0144$ ).

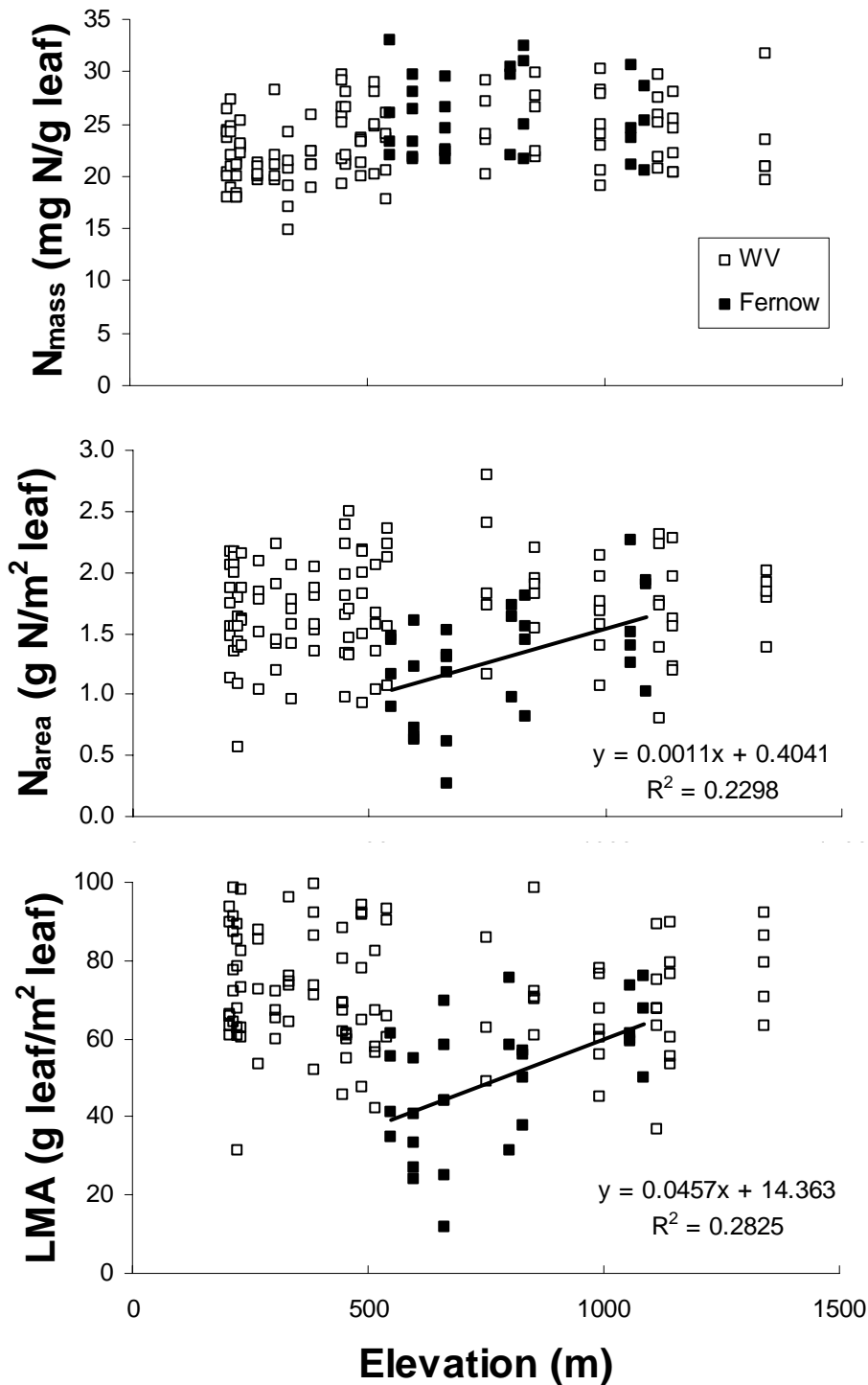


Figure 4.5. Whole ecosystem trends of foliar [N] on a mass basis ( $N_{\text{mass}}$ ), foliar [N] on an area basis ( $N_{\text{area}}$ ), and leaf mass per area (LMA) at two spatial scales (Fernow Experimental Forest [Fernow] and West Virginia [WV]). Lines are fitted to show the separate relationships of  $N_{\text{area}}$  and LMA with elevation in the Fernow. Each point represents a plot mean.

## DISCUSSION

The range of foliar N concentrations of the dominant trees in Central Hardwood forest ecosystems were consistent across the state of West Virginia but more detailed observations along elevation gradients reveal important differences among species and different spatial scales. We found that not all species respond to elevation in the same manner. Although species differences in foliar N were observed at both spatial scales, the response of foliar to elevation change was more dynamic among species at the statewide scale. Similarly, studies that have examined foliar N of deciduous forest tree species in the northeastern U.S. also found that different species responded differently in response to elevation (Ollinger and Smith 2005, Aber *et al.* 2003). In a study of the Tibetan Plateau, Luo *et al.* (2005) observed that  $N_{area}$  and LMA of conifer species increased with elevation but  $N_{area}$  and LMA relationships to elevation were not as strong for hardwoods. These studies indicate that species composition is an important determinant of ecosystem productivity and nutrient budgets.

Both C and N concentrations in the canopy of the Fernow were higher than statewide means suggesting that this particular locality represents the high end of a nutrient status gradient in the state. This N status would likely be detected with large scale sampling or remote sensing studies. The result that may be more important for regional productivity estimates is the difference in canopy foliar  $N_{area}$  and LMA with elevation at the local scale. The incongruence of elevation related changes in morphology and physiology between spatial scales may have profound implications for regional productivity estimates.

Our study also revealed  $N_{mass}$  averages at both spatial scales that are higher than the foliar N concentrations reported in other studies of Eastern U.S. forests (Table 4.2; Martin and Aber 1997, Mitchell *et al.* 1999, Reich *et al.* 1999a, Ollinger *et al.* 2002, Ollinger and Smith 2005) and of other forest regions with similar tree species (Martin and Aber 1997, Reich *et al.* 1995, Reich *et al.* 1999a). We found that leaf  $N_{mass}$  in the Fernow was 21%

TABLE 4.2. Published foliar nitrogen concentrations for species common to Central Appalachian forest.

Location	Species	Foliar N (mg N/g leaf)	Source
NC	Red maple	18.4	Reich <i>et al.</i> 1999
NC	Yellow birch	17.8	Reich <i>et al.</i> 1999
NH	Beech-Birch	21.3	Ollinger <i>et al.</i> 2002
NH	Sugar maple	22.7	Ollinger <i>et al.</i> 2002
NH	Maple, beech, birch	19.8	Ollinger and Smith 2005
NH	Beech dominated	21.7	Smith <i>et al.</i> 2002
NH	Yellow birch dominated <sup>+</sup>	22.0	Smith <i>et al.</i> 2002
NH	Red maple dominated <sup>+</sup>	20.0	Smith <i>et al.</i> 2002
NH	Sugar maple dominated <sup>+</sup>	20.6	Smith <i>et al.</i> 2002
NC	Red maple	18.0	Mitchell <i>et al.</i> 1999
NC	Birch species	19.5	Mitchell <i>et al.</i> 1999
NC	Hickory species	24.5	Mitchell <i>et al.</i> 1999
NC	Ash species	19.2	Mitchell <i>et al.</i> 1999
NC	Yellow poplar	21.3	Mitchell <i>et al.</i> 1999
NC	White oak	23.2	Mitchell <i>et al.</i> 1999
NC	Red oak	28.7	Mitchell <i>et al.</i> 1999
NC	Basswood	28.8	Mitchell <i>et al.</i> 1999
WI	Red maple	21.0	Reich <i>et al.</i> 1999
WI	Sugar maple	18.5	Reich <i>et al.</i> 1999
WI	Black cherry	20.7	Reich <i>et al.</i> 1999
WI	Hickory	19.8	Reich <i>et al.</i> 1999
WI	White ash	19.8	Reich <i>et al.</i> 1999
MA	Red oak-Red maple	21.4	Martin and Aber 1997
WI	Sugar maple dominated <sup>+</sup>	23.9	Martin and Aber 1997
WI	Basswood dominated <sup>+</sup>	26.1	Martin and Aber 1997
WI	Red oak dominated <sup>+</sup>	23.5	Martin and Aber 1997
WI	White oak dominated <sup>+</sup>	24.8	Martin and Aber 1997
WI	Red maple dominated <sup>+</sup>	23.7	Martin and Aber 1997
WI	Red maple	19.5	Reich <i>et al.</i> 1995
WI	Sugar maple	17.6	Reich <i>et al.</i> 1995
WI	Hickory	19.8	Reich <i>et al.</i> 1995
WI	White Ash	21.3	Reich <i>et al.</i> 1995
WI	Black cherry	20.7	Reich <i>et al.</i> 1995
WI	Red oak	21.1	Reich <i>et al.</i> 1995
	Overall average	21.5	

<sup>+</sup> Forested plot sampled was dominated by the indicated species but included some other species

higher than the average  $N_{\text{mass}}$  reported in past literature and, across WV,  $N_{\text{mass}}$  was 8% higher than the reported average. Thus, there may be important implications of these results for regional studies that have extrapolated forest characteristics across the Central Appalachian region (Aber *et al.* 2003, Pan *et al.* 2004, Hom *et al.* 2006). Historically, the Central Appalachian region has received higher concentrations of N deposition than other forests in the U.S. where foliar N has been described (Ollinger *et al.* 1993, US EPA 2002, US EPA 2006). This is likely the source of the additional N that was observed at the watershed scale as well. Past studies have described forest N differences along N deposition gradients in the U.S. (Ollinger *et al.* 1993, Lovett and Rueth 1999, Nadelhoffer *et al.* 1999, Aber *et al.* 2003) but have not characterized variation that exists in foliar N with small scale elevation changes in Central Appalachian forests.

Trends in soil carbon and N may be related to some of the foliar N observations. Soil N concentrations in the Fernow were sometimes more than double the concentrations that were observed across West Virginia (Table 4.1), and the %N in the soil was consistently different between the two spatial scales regardless of elevation or species. Since soil C:N is negatively correlated with nitrification rates and nutrient retention (McNulty *et al.* 1991, Lovett and Rueth 1999, Lovett *et al.* 2002, Ollinger *et al.* 2002), it is likely that soil C:N at different elevations determines nutrient uptake and explains the observed  $N_{\text{area}}$  variation. Bulk density, a metric that is correlated with nutrient retention, was also lower in the Fernow than across the state and declined with elevation at the watershed scale while remaining consistent across the statewide scale. Aber *et al.* (2003) found that nitrification rates were correlated with elevation, but in our study total soil N was consistent across elevations in the Fernow. It is actually variability in soil C that caused the soil C:N trend. This trend of increasing soil C with altitude has not been described to our knowledge and is likely due to the relatively shallow soil found at higher elevation in the Fernow. Other studies have concluded that accumulating belowground carbon is

deposited vertically (Jobaggy and Jackson 2000). Thus we suggest that, in the case of shallow soil, more C remains closer to the soil surface.

Alternatively, it may be species composition that controls the variation in soil conditions with elevation (Lovett *et al.* 2002). Species level harvest is particularly relevant in West Virginia because most of the state forest land is privately owned mature timberland (Griffith and Widmann 2003) that will likely be subject to a range of harvest practices in the near future. Since soil is a substantial sink for terrestrial carbon, differences in soil C among harvestable tree species across the topography of the Central Appalachian region should be included in models of land use change. For example, *Acer saccharum* and *Prunus serotina* have different economic values (Emanuel and Rhodes 2005), and are also associated with different carbon storage potentials. Selective removal of the more valuable *Prunus* trees from a forested ecosystem would have different consequences for the terrestrial carbon budget than removal of *Acer* trees. Soil that was sampled from the forest floor near *Quercus rubra*, another valuable harvest species, appears to be important for driving elevation related soil changes as well. This was the only tree species that was associated with an increase in soil N along the elevation gradient in the Fernow.

If we are interested in changing species composition within an ecosystem, then there are important elevation effects on the canopy to consider along with effects on soil. Variation in foliar N with elevation was observed in canopy leaves from *Acer*, *Quercus*, and *Carya* species which are all timber species with varying economic values. Inter-specific differences in nitrogen pools and cycling across the landscape are indicative of ecosystem productivity differences that are likely to result if preferential logging of valuable species or easily accessible elevations is employed in this region.

## CONCLUSIONS

For regionally scaled estimates of foliar quality and productivity rates in WV, species variation in the relationship between foliar N concentrations and elevation may be inconsequential. However, more detailed spatial variation exists that may influence the accuracy of such regional estimates. At both spatial scales studied here, species differences in foliar N would be important for determining changes in ecosystem structure and productivity in response to community composition shifts and selective harvests. For some canopy trees, including valuable harvest species like oaks (*Quercus* spp.) and maples (*Acer* spp.), there were significant changes in foliar N with elevation that were not observed for all species and are indicative of productivity and carbon sequestration differences.

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## **Chapter 5**

### **Carbon sequestration over a century of forest regeneration in the Central Appalachian region**



## ABSTRACT

Central Appalachian forests have been under-represented in studies that aim to quantify carbon storage of terrestrial systems in the Eastern United States. West Virginia is at the heart of the Central Appalachian region and has 12 million acres of mature forestland that have been regenerating since the early 1900's. This study estimated historical rates of carbon sequestration in the forestland of West Virginia using the PnET-CN and PnET-CN<sub>sat</sub> models. Over the past century, the carbon sink in this region was between 0.24 and 0.31 PgC and the rate of carbon sequestration was about a third of the rate that has been projected for temperate forests in other studies. Nitrogen saturation, a process that has been observed in parts of Central Appalachia may stimulate carbon sequestration by 20%. Forests in this region are an active carbon sink, but may be counter-balance less of the atmospheric CO<sub>2</sub> rise than has previously been suggested.

## INTRODUCTION

According to the latest Intergovernmental Panel on Climate Change Report (2007), the net global terrestrial carbon sink since the dawn of the 21<sup>st</sup> century has been about 0.1 Pg C/yr (Denman et al. 2007). Temperate forests are considered to be a substantial portion of this terrestrial carbon sink (Heath et al. 1993, House et al. 2002, Houghton 2003a, Pregitzer and Euskirchen 2004), but there is significant debate over the amount of carbon that has been stored in growing forests and how terrestrial carbon will change in response to future land use (Sedjo 1993, Schimel et al. 2000, House et al. 2002, Houghton 2003b). With approximately 212 million hectares of forest, the United States of America is the third most forested nation in the northern hemisphere (Goodale et al. 2002). Most of the nation's forests are in the Eastern and South Central regions of the country, much of which is temperate deciduous forest (Turner et al. 1995).

Central Appalachian forests have been under-represented in studies that aim to quantify carbon storage of terrestrial systems in the Eastern United States. West Virginia is at the heart of the Central Appalachian region and has 12 million acres of mature forestland that have been regenerating since the early 1900's. West Virginia is also located in the transition zone between oak-hickory and beech-maple-birch forest types (Iverson and Prasad 2001). These qualities make it a unique region that is likely to be susceptible to forest productivity changes in the near future due to forest conversion in response to changes in the economic value of wood products (Emmanuel and Rhodes 2005, Parker et al. 2007) and species range shifts associated with climate change (Parmesan and Yohe 2003).

The objectives of this study were to estimate the historical rates of carbon sequestration across West Virginia and to assess the degree to which climatic variation around the state impacts productivity and terrestrial carbon storage. Due to spatial variation in foliar and soil N concentrations (discussed in Chapter 3), I estimated the carbon storage of forested sites in WV using two versions of the PnET suite of models; one that assumes Stage 2 N saturation (PnET-

CN<sub>sat</sub>) and one that assumes a less N-saturated state (PnET-CN). This study thus provides a baseline value of the amount of carbon stored in the Central Appalachian region with and without N-saturated conditions.

## METHODS

I established four transects of forested sites located along a range of elevations (~200 to 1400m) in the state of West Virginia. Each transect ran east to west across the state to maintain a similar latitude with an average distance between sites of 80 km (Figure 5.1). A total of 19 sites were identified (Table 5.1) that were comprised of mature, closed-canopy deciduous forests with canopy trees at least 30 cm in diameter at breast height. The top ten most abundant canopy trees in the state were identified from U.S. Forest Service records and canopy foliage was collected from at least five of these dominant canopy species at each sampling site using a 12-gauge semi-automatic shotgun. The species sampled included *Acer rubrum*, *Acer saccharum*, *Carya* spp., *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Prunus serotina*, *Quercus alba*, *Quercus rubra*, and *Tilia americana*. Intact leaves were obtained from the small twigs from the top of the canopy and leaf disks were cut, dried for 48 hours at 65°C, and weighed so that leaf mass per area (LMA) could be calculated. Soil samples were collected from the A horizon at four locations within 2 m of the base of each tree using a 1.9 cm diameter soil corer. The four soil samples from each tree location were combined, dried for 48 hours at 65°C and weighed. Bulk density of the soil was calculated as the dry mass per volume of soil. All dried soil and leaf tissue samples were analyzed using Dumas combustion in a Carlo Erba CN autoanalyzer (Fisons Instr., Milan, Italy) to measure carbon and N content.



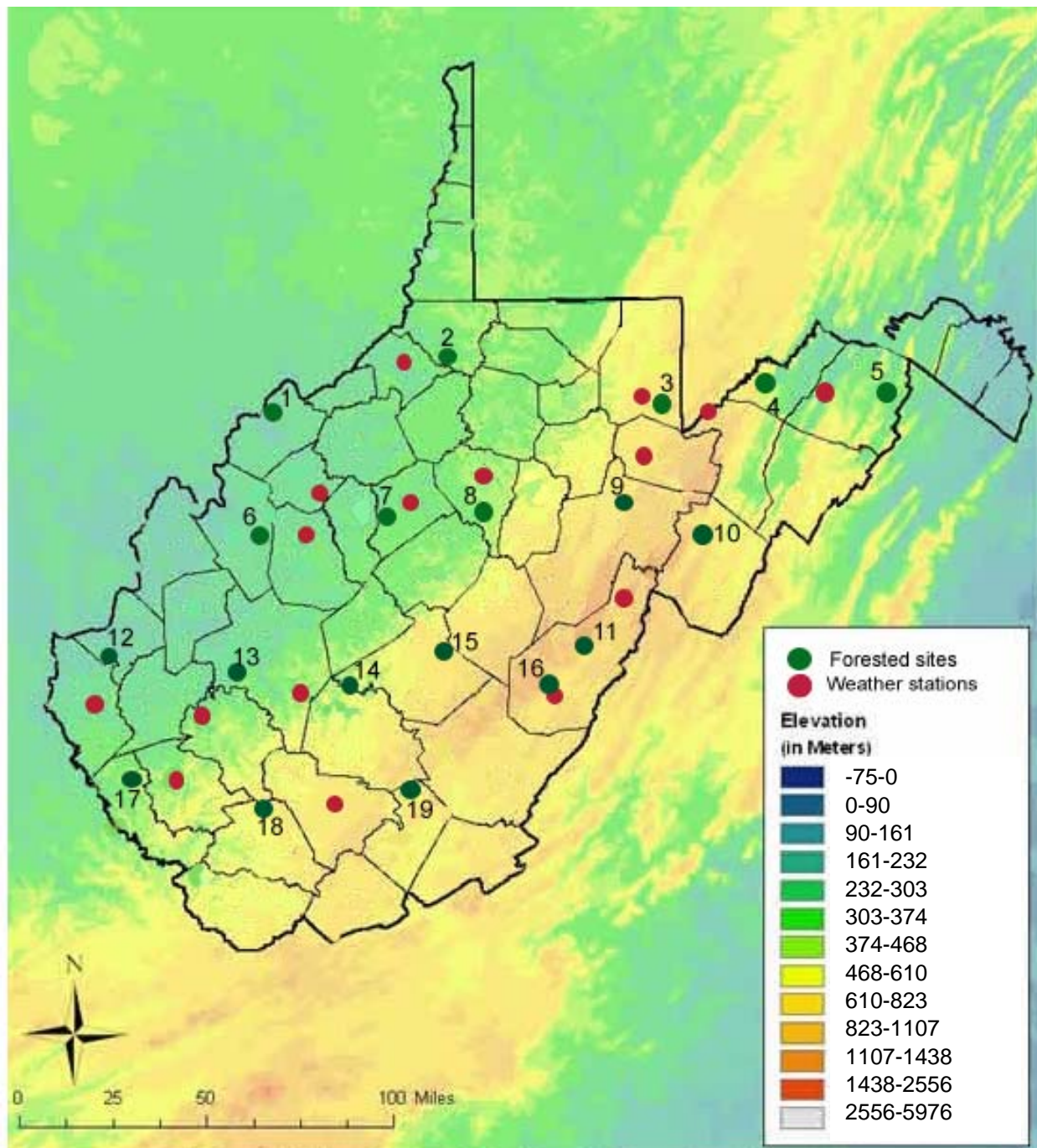


Figure 5.1. Map shows the locations of all forested sites sampled and weather stations that were the sources of the climate data for parameterizing the climate history for different parts of the state. (Map adapted from West Virginia Climate Center map of National Weather Service COOP stations)

Latitude, LMA, and soil N concentrations were used as inputs in the PnET-CN<sub>sat</sub> model to parameterize each model run for a particular forest site. Other input parameters were assigned according to measurements in the Fernow Experimental Forest as defined in Chapter 1 (Table 1.1). I parameterized the model for each site according to climate data from the closest weather station that had historical climate records dating back to at least 1949 (Figure 5.1). Three of the weather stations had climate records dating back to 1927, one had records starting in 1926, and another starting in 1937. Three of the weather stations were applicable to two experimental sites each so that sites 10 and 11 were parameterized with the same climate data, sites 14 and 15 were parameterized with the same climate data, and sites 18 and 19 were parameterized with the same climate data. Climate history was reconstructed for unmeasured years using monthly averages from all the years for which climate data was available. I reconstructed climate accordingly to run the model starting in 1900. I included a 70% biomass removal event in 1908 to account for the logging that occurred during that time and 25% biomass removal in 1935 to account for losses due to the Chestnut Blight (Hicks 1998). Atmospheric CO<sub>2</sub> was ramped according to Mauna Loa observations and nitrogen deposition was ramped according to N deposition amounts reported by the National Atmospheric Deposition Program for Parsons, WV (NADP 2007). The same routines for CO<sub>2</sub> and N deposition were used for all sites.

The full validation of PnET-CN<sub>sat</sub> for the Central Hardwood Region was conducted in the Fernow Experimental Forest (Chapter 1). This forest shows symptoms of N saturation (Peterjohn et al. 1996) that may not be common to all sites in West Virginia (Chapter 3), so I also ran the original PnET-CN model for all the sites to assess the relative difference in productivity that would result without N-saturated conditions. I ran this version of the model with parameters that were measured in the N-saturated forest and then again using default N parameters that were published for similar forest types that were less N-saturated (Aber et al. 1997).

Foliar N concentrations were used as a validation test for model outputs from PnET-CN<sub>sat</sub> and PnET-CN. The models each predict foliar N concentrations on an annual basis but the variability from year to year is typically low, so I compared measured foliar N to the average foliar N for the last 20 years of the model run. I compared the estimates of foliar N from each of the three different model runs to the mean foliar N concentration that was measured in canopy leaves at each site using a 2-way ANOVA and a Tukey-Kramer HSD. I then estimated net ecosystem productivity (NEP) for each site and tested the variation in model estimates of NEP by site using a nested 2-way ANOVA with model type and transect as the main effects and site nested by transect. All statistical analyses were calculated using SAS-JMP software version 5.1.

## RESULTS

The accuracy of modeled foliar N concentration estimates could not be validated for all of the forested sites (Figure 5.2). The model estimates of foliar N that were most similar to measured foliar N were generated using the original PnET-CN model that was parameterized according to N conditions similar to temperate deciduous forests that were *not* N-saturated; estimates from this model method were similar to measured values for sites 3, 4, 9, 10, 11, 14, 18, and 19. The inaccuracy of the predictions of PnET-CN varied by site ( $F = 6.45, p < 0.0001$ ), ranging from less than 1% to 35% greater than measured foliar N estimates. All of the model runs over-estimated foliar N, but the original PnET-CN model with full parameterization from a Stage 2 N-saturated forest was consistently the least accurate predictor for any forest sites and overestimated foliar N by 45% on average. The degree to which this model run overestimated also significantly differed among sites ( $F = 24.32, p < 0.0001$ ). PnET-CN<sub>sat</sub> model estimates of foliar N were 31% greater than measured estimates on average with significantly different performance among sites ( $F = 11.49, p < 0.0001$ ), and was validated against foliar N measurements in site 18 only.

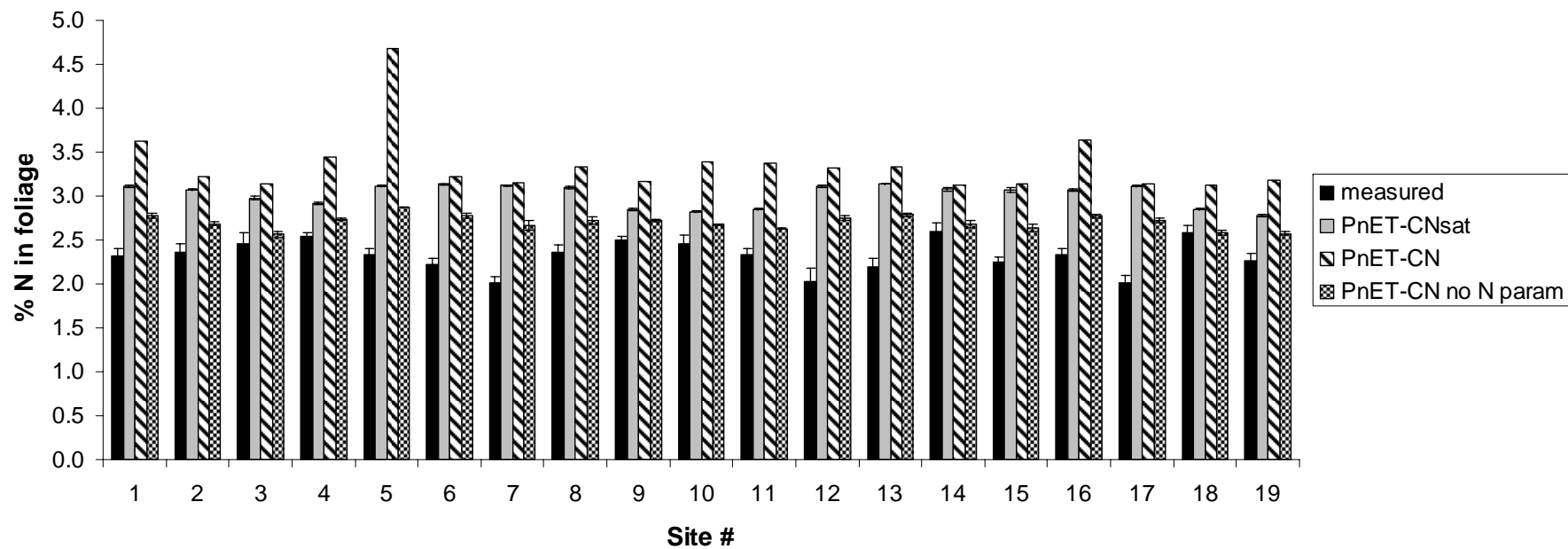


Figure 5.2. Foliar N estimates from forested sites in West Virginia as estimated from on-site measurements (black) and with three different model runs: PnET-CN<sub>sat</sub> with N parameters specified according to Stage 2 N saturation (gray), PnET-CN with N parameters specified according to Stage 2 N saturation (striped), and PnET-CN with N parameters specified according to forests in earlier stage of N saturation (checkered). Error bars represent standard error.

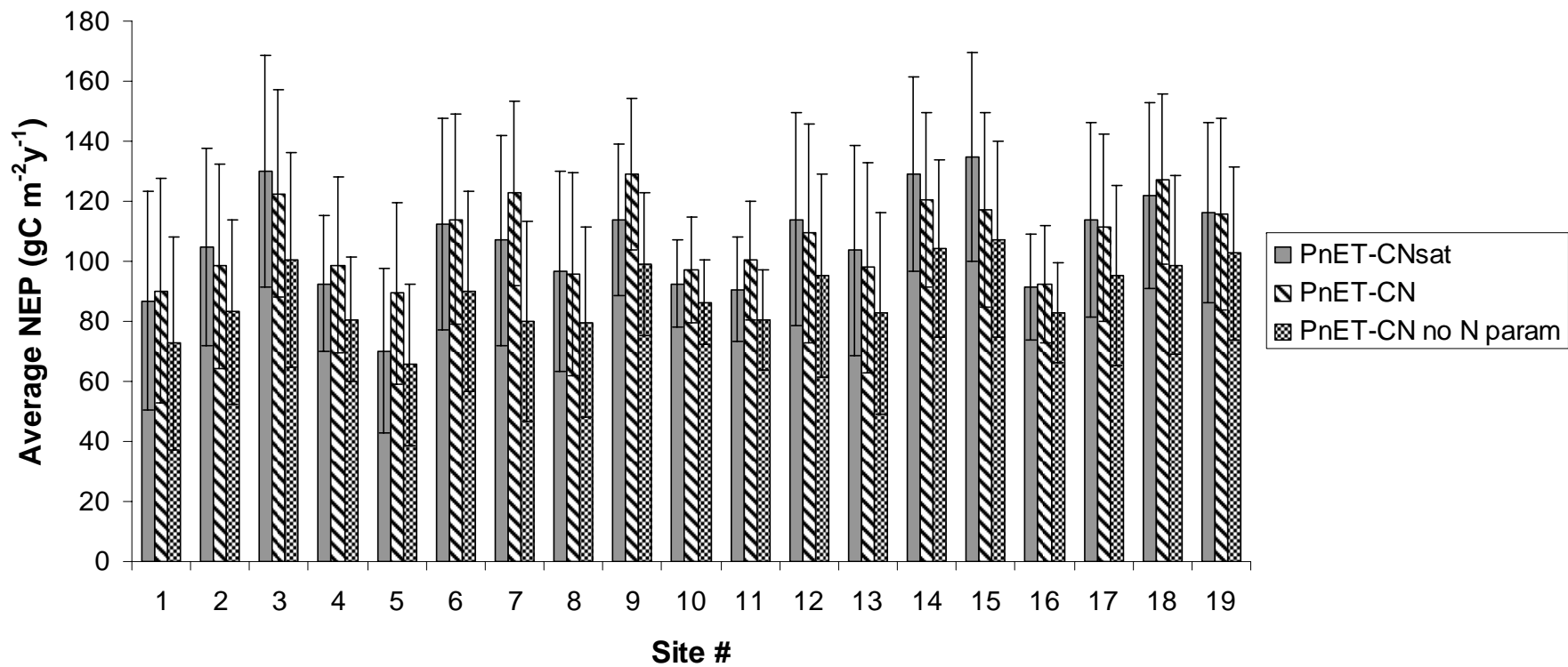


Figure 5.3. Net ecosystem productivity (NEP) estimated for forested sites in West Virginia with three different modeling methods: using PnET-CN<sub>sat</sub> with N parameters specified according to Stage 2 N saturation (gray), using PnET-CN with N parameters specified according to Stage 2 N saturation (striped), and PnET-CN with N parameters specified according to forests in earlier stage of N saturation (checkered). Each bar represents the mean NEP over a 54 year period. Error bars represent standard error.

The range of nitrogen processes that likely control N pools across the Central Appalachian region are not reflected in the parameters and model routines I applied. Thus, NEP estimates of these sites are theoretical comparisons of two scenarios: first, if all deciduous forests in WV were in Stage 2 of N saturation and, second, if all deciduous forests in the same region were in an earlier stage of N saturation. These modeling scenarios produced significantly different estimates of NEP ( $F = 11.38$ ,  $p = 0.0002$ ; Table 5.1). Modeled estimates of NEP using PnET-CN<sub>sat</sub> were generally 20% higher than estimates of NEP with PnET-CN (Figure 5.3). There were also significant differences in NEP estimates among forest sites around the state regardless of the modeling method ( $F = 15.06$ ,  $p < 0.0001$ ; Table 5.1), but there were no differences in NEP detected among transects ( $p = 0.4442$ ).

Table 5.1. Statistical result of a nested 2-way ANOVA test of the effects of model method, transect, and site on NEP estimates with site nested as a random effect within the latitude treatment. Latitudinal differences are defined by transect distinctions.

Effect	SS	MS	Df	F	<i>p</i>
Model method	30808	15404	2	11.3825	0.0002
Latitude	57693	19231	3	0.9438	0.4442
Site(latitude)	305642	20376	15	15.0568	<0.0001
Model method x Latitude	8559	1427	6	1.0541	0.4113
Model method x Site(Latitude)	40599	1353	28	0.0526	1.0000

The highest NEP was estimated for site 15 according to both models (Figure 5.3). This site was located in the central part of West Virginia at a moderate elevation of 539m (Figure 5.1). There were no general spatial trends in productivity differences across the state. For example, sites 18 and 19 were two of the southernmost sites and had high NEP but ranked similarly in productivity to sites 14 and 3 which were central and north-central to the state, respectively. The lowest productivity was observed in site 5, located in the eastern panhandle. Total carbon stored over the past 54 years was highly variable among the 19 sites; the range was 3490 gC/m<sup>2</sup> according to PnET-CN<sub>sat</sub> and 2260 gC/m<sup>2</sup> according PnET-CN. NEP estimates indicated that all forested sites were active sinks of carbon during this time. The total carbon

stored since 1950 averaged across all 19 sites was approximately  $4790 \text{ gC/m}^2$  with no N saturation simulated (PnET-CN) and  $5749 \text{ gC/m}^2$  with Stage 2 N saturation simulated (PnET-CN<sub>sat</sub>), indicating a potential stimulation of carbon storage of approximately 20% by N deposition. The estimated carbon fluxes across the forested area of West Virginia were approximately 4.3 Tg C/yr according to PnET-CN and 5.2 Tg C/yr according to PnET-CN<sub>sat</sub>.

## DISCUSSION

Over the 54 years that NEP was modeled using on-site climate records, the total carbon stored in the 48590 sq km of forested land in West Virginia was estimated to be between 0.23 and 0.28 PgC depending on whether the model assumed the forests were N-saturated or not. If one considers the entire 95 years since logging occurred across the state in the early 1900's, the total carbon stored during the regeneration of WV forests was estimated to be between 0.24 and 0.31 PgC (the progressive accumulation is shown in Figure 5.4). The higher estimates of carbon sequestration reflect the NEP stimulation in response to nitrogen saturation while the lower estimates reflect NEP with little or no N saturation. My study indicates that the Central Appalachian forests are, thus, a net carbon sink and have been over the past century. Forests around the region vary in levels of nitrogen saturation, a process that may stimulate carbon storage by 20% on average.

The modeled estimates of the annual rate of carbon sequestration in West Virginia represents 5.4 to 6.5% of the total annual carbon sink of terrestrial ecosystems in the U.S. (Schimel et al. 2000). However, the amount of carbon stored for a given area in West Virginia is only about one third of that observed in other temperate forests (Table 5.2). Previous estimates have ranged from about 15 to 20 kgC/m<sup>2</sup>. At the high end of estimates, Turner et al. (1995) determined that carbon storage in forests in the Northeastern U.S. was higher than the average

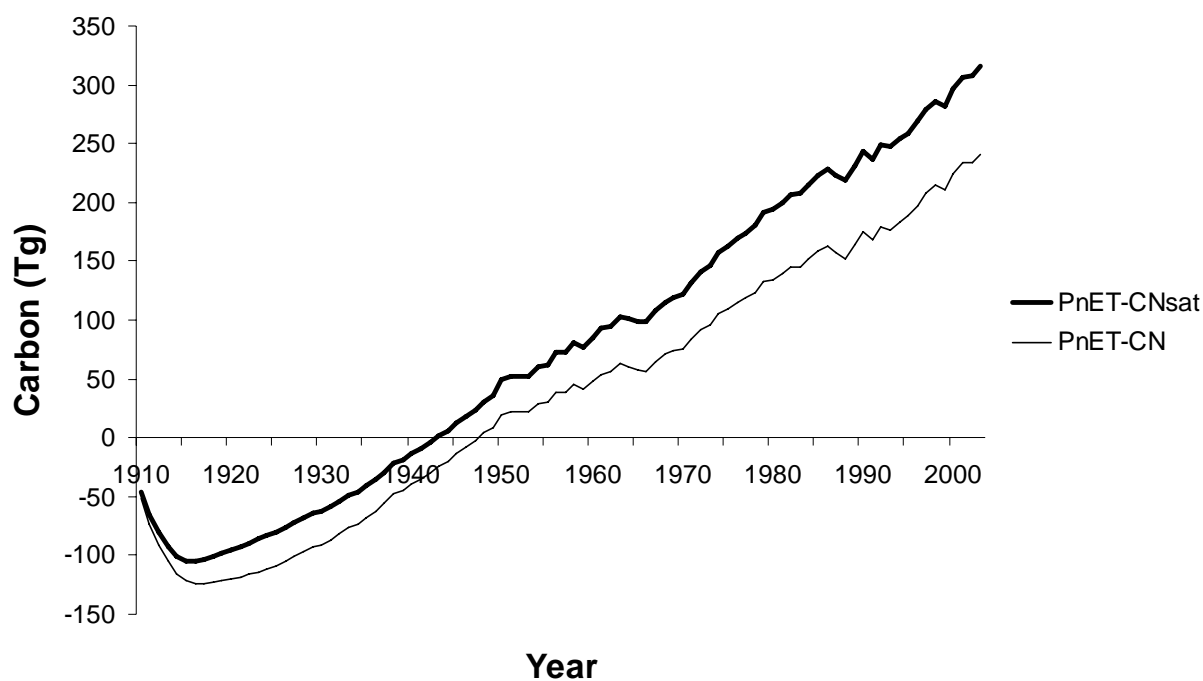


Figure 5.4. Progressive accumulation of carbon in West Virginia forests (Tg C) following a logging period in the first decade of the 20<sup>th</sup> century as predicted by the PnET-CN<sub>sat</sub> and PnET-CN models. Lines represent mean estimates of the productivity for 19 forested sites. The average difference between estimates from the two models over 95 years represents a 16% stimulation in response to N saturation.



terrestrial C sequestration projected for the conterminous U.S. (Goodale et al. 2002) or for temperate forests worldwide (Heath et al. 1993, House et al. 2002, Pregitzer and Euskirchen 2004). Our modeled estimates indicate that these may be overpredictions or, if the other studies are correct, they suggest that topographic or edaphic conditions of the deciduous forests of West Virginia might limit their productivity. My study indicates that forests in the Central Appalachian region may counter-balance less of the atmospheric CO<sub>2</sub> rise than has previously been suggested.

Table 5.2. Estimates of terrestrial carbon storage from literature values and this study.

	Fluxes (PgC/yr)	Pools (kgC/m <sup>2</sup> )	Source
Northeastern U.S. forestland (including WV)		20.0	Turner et al. 1995
Conterminous U.S. forestland		16.8	Goodale et al. 2002
Global temperate forests		16.5	Heath et al. 1993
Global temperate forests		15.3	House et al. 2002
Global 71-120 yr. old temperate forests		18.9	Pregitzer and Euskirchen 2004
Global 71-120 yr. old temperate forests*		15.8	Pregitzer and Euskirchen 2004
West Virginia forestland (not N-saturated)		4.79	
West Virginia forestland (N-saturated)		5.75	

\*Distinguished from first Pregitzer and Euskirchen estimate which was calculated from flux measurements: second estimate was calculated from ecosystem components.

Modeled estimates of foliar N in the canopy of deciduous forests in West Virginia were highly variable and did not accurately predict measurements across the state. Measured foliar and soil N vary statewide and many studies have shown a high degree of variability in N with topography and spatial scale (Aber et al. 2003, Pan et al. 2004, Luo et al. 2005, Ollinger and Smith 2005). While N-saturated conditions have been documented in some forests of West Virginia (Peterjohn et al. 1996), it is likely that much of West Virginia is not nitrogen-saturated. The relative differences in modeled foliar N for several sites (1, 4, 5, 9, 10, 11, 16 and 19) were similar to the differences in foliar N output obtained with the same models for the Fernow Experimental Forest in Chapter 1. Using PnET-CN with N-saturated parameterization, predictions of foliar N for these sites were between 11 to 50% greater than prediction made with

PnET-CN<sub>sat</sub> (Figure 4.2). Model predictions of foliar N using PnET-CN with N-saturated parameterization were less than 10% different than prediction made with PnET-CN<sub>sat</sub> in all other sites (2, 3, 6, 7, 8, 12, 13, 14, 16, 18).

The response of the model outputs to site variability suggests a pattern that indicates a group of sites around West Virginia that resemble the N-saturated conditions of the Fernow Experimental Forest (1, 4, 5, 9, 10, 11, 16 and 19) while the other sites are indicative of less saturated conditions (2, 3, 6, 7, 8, 12, 13, 14, 16, 18). On-site measurements are necessary to completely determine the correct N parameters for the PnET-CN<sub>sat</sub> model. Interestingly, all of the sites identified for potential N saturation are located in the northernmost transect or along the eastern edge of the state. This pattern may be indicative of climate patterns that are correlated with latitude in the case of the northern sites and elevation in the case of the eastern sites. This pattern may also be related to species composition differences as well because West Virginia lies on the boundary between oak-hickory dominated forest and maple-beech-birch dominated forests (Finzi et al. 1998, Lovett and Rueth 1999, Verchot et al. 2001, Venterea et al. 2003). Nitrogen cycling differences have been repeatedly observed as distinct between these forest types, particularly with regard to maple and oak which are associated with the highest and lowest rates of nitrification respectively (Lovett and Mitchell 2004).

Overall, West Virginia forests act as sinks for atmospheric carbon dioxide. The quantity of this sink depends on the stage of nitrogen saturation that applies to the region as a whole because N saturation appears to stimulate carbon sequestration by 20%. Climate variability, topography, and species composition differences around the state also contribute to spatial variability of terrestrial carbon sinks. Generally speaking, the carbon storage capacity of this region is lower than projections that have been made for the larger surrounding region and similar forest types. Since these results dispute the larger body of literature on carbon sequestration, it is essential to improve the rigor of model parameterization and validation in this

region. The results presented here would be strengthened by conducting more validation tests of outputs for other ecosystem components that are important for productivity and carbon sequestration.

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## Chapter 6

### CONCLUSION



The story of Central Appalachian forest productivity has unfolded to reveal some new information about temperate forest carbon sequestration in the United States. Unique qualities of West Virginia forests have been exposed and contribute to productivity rates that are lower than projections made for this biome as a whole. The goal of my research was to develop a model to predict the potential carbon storage in the temperate deciduous forests in the Central Appalachian Mountains. Using the PnET-CN<sub>sat</sub> model (Davis et al. *in review*), my research suggests that, despite the high nitrogen availability that was observed, the forests in Central Appalachia have grown at only a moderate pace relative to similar forest types in other temperate regions of the world. The regeneration of West Virginia forests over the last century has amounted to a consistent C sink, but these ecosystems did not sequester a higher amount of C than has previously been suggested and the amount of C sequestration cannot explain some of the imbalances in the global carbon budget that have been proposed (Sedjo 1992, Schimel 1995).

Generally, I found that over the century of regeneration following harvest, forests in the Central Appalachian region sequestered 4 to 5 Tg C yr<sup>-1</sup>. The amount of carbon storage is stimulated up to 20% by N saturation. In addition, carefully planned harvests can also stimulate forest productivity by as much as 37%. The overall contribution of forest regeneration and growth enhancement by anthropogenic sources of C and N to the global carbon sink is not great enough to counter-balance the increasing rise in atmospheric carbon dioxide. Loss of these forests due to deforestation would add a source of carbon to the atmosphere of about 300 Tg that would take between 50 and 100 years to recover.

One of the goals of my research was to measure foliar N throughout the state of West Virginia. Through this effort, I found higher concentrations of foliar N in West Virginia forests than has been observed in surrounding regions, which suggests higher rates of photosynthesis and gross primary productivity. The ecosystem productivity estimates that were produced with the PnET-CN model, even after accounting for nitrogen saturation, suggest that this region

may be subject to lower nitrogen use efficiency than is typical for temperate deciduous forests. N deposition rates reached a plateau in the last decade such that there is no longer a progressive increase in N inputs (US EPA 2006). There are still high N additions to the forest, but rates of N deposition have remained steady over the last decade due to stricter emissions standards (US EPA 2002). Carbon dioxide concentrations on the other hand continue to increase due to fossil fuel burning. Thus, the shifting ratio between carbon and nitrogen that is available to the ecosystems in the Central Appalachian region may have consequences for nutrient use efficiency and productivity in the future (Luo et al. 2004, Finzi et al. 2006).

Some harvesting practices may stimulate carbon sequestration over a long-term period (ie. 50 years or more), especially if wood resources from harvesting events are used for long-lived products. The harvesting practices that I found to have the greatest stimulation effect on carbon sequestration, diameter-limit cuts and selective cuts, require planning and foresight that may not be characteristic of most private landowner forest management practices. It has been documented that non-professional forestry practices can lead to “high-grading,” or a reduction in forest site quality in response to removal of the more valuable trees in a size class (Hicks 1998). The harvested forests that were examined during this research were managed by the USDA Forest Service and timber harvest was conducted by professional foresters that were trained to follow best management practices for each harvest type. Usually, the goal of the best management practices is to maintain a sustainable forest resource after each cut such that there are conditions for a forest of equal quality to regenerate. If a private landowner has mature saw-timber on land that has regenerated over the last century, it is unlikely that the landowner will make repeated harvests with the long-term goal of maintaining the species composition of the dominant canopy trees. It is more likely that a logger would be commissioned to harvest a certain percentage of trees for profit. The landowner would have little to do with species selection and the economic benefits for both parties would outweigh any motivation to maintain species



composition. Most of the forestland in West Virginia is privately owned and most land owners are not educated in best management practices for forestry. The research presented here suggests that the sustainability of the state's forest resources might depend on outreach efforts that educate land-owners about best management practices and the balances that exist between economic and environmental benefits associated with sound forest harvesting strategies.

I have observed that species are not equal in their contribution to forest productivity mainly through the investigation of spatial variation in nitrogen concentrations among species. Species differences played a rather minor part in the research that has been presented but the broader view of regional productivity reveals that species differences may be a key part of the ecological processes that control productivity in the Central Appalachian region. One reason is that different tree species have different economic values in the wood product market. Another reason, that is even more important from an ecological perspective, is that nutrient cycling differences have been correlated with tree species. Sugar maple, in particular, has been identified as dominating soils that have high nitrification rates (Finzi et al. 1998, Lovett and Rueth 1999, Verchot et al. 2001, Christ et al. 2002, Venterea et al. 2003). While it is still unclear whether tree species control soil nitrogen conditions or just have different tolerance ranges (Lovett and Mitchell 2004), it is evident that tree species composition is linked to differences in soil nitrogen transformations. This means that economically driven harvests that favor particular species are likely to result in a different ecosystem nutrient status and different productivity rates.

In the statewide C modeling exercise, it became apparent that nitrogen availability and ecosystem processes are variable around the state. Forest sites in the northern and easternmost parts of West Virginia were distinguished from the other forested sites around the state. Recent Forest Inventory Analysis (FIA) data as summarized by Iverson and Prasad (2001) suggest that a boundary between dominant forest types exists in West Virginia and that the northern and eastern parts of the state are maple-beech-birch dominated forests, while the remainder of the

state is dominated by oak-hickory forests. This presents an interesting view of the productivity differences across the state in a context of nitrogen availability. If maple-dominated forests are accelerating the nitrification process of ecosystems in the region (Lovett and Mitchell 2004), then species selection for harvest may have even more important implications for forest nutrient cycling and productivity. By selecting maples for harvest, the process of N saturation might be abated, while selecting preferentially for oak or cherry because of their economic values may accelerate N saturation. On the other hand, if maples are more tolerant of N-saturated conditions that are occurring due to processes controlled by climatic, topographic, microbial and/or edaphic conditions, then selective harvest of maples would induce an accelerated reduction of productivity through species diversity loss and intolerable nutrient conditions for the post-harvest forest stand.

The land of West Virginia is mostly forested and the ecosystem consists of unique nutrient qualities, species compositions, and economic values relative to the terrestrial ecosystems of the surrounding region. The research I have presented serves to describe how these unique attributes affect the forest carbon budgets of the Central Appalachian region. Climate, anthropogenic pollutants, and land management significantly influence the productivity of forests in West Virginia such that the inevitable changes in these forces over time are likely to alter the processes that control forest productivity in the future. With continued advances in our understanding of complex ecological systems and their interactions with the economic forces that regulate anthropogenic pressures on natural systems, we will gain knowledge about how to ameliorate the losses of resources provided by forested landscapes.

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## RESEARCH INTERESTS

- Forest carbon sequestration differences associated with forest age, land use, and invasive species
- Physiological ecology of forests in responses to harvest and anthropogenic pollutants
- Ecosystem models of carbon and nitrogen cycling with human-environment feedbacks
- Dendrochronology and historical climate reconstruction

## PROFESSIONAL EXPERIENCE

### REGIONAL MATH/SCIENCE CENTER

of FROSTBURG STATE UNIVERSITY, Frostburg, MD

1997-2003

*Assistant Director* (1999-2003)

*Curriculum and Activities Assistant* (1999)

*Head Resident/ Weekend Activities Coordinator* (1998)

*Tutor/Counselor* (1997)

- Supervised and managed academic program
- Recruited students and staff
- Interviewed, hired, and trained residential and teaching staff
- Developed curriculum (environmental science and renewable energy topics)
- Coordinated and supervised weekend trips for 50-60 people
- Designed environmental science research projects with field data collection

AMERICAN ASSOCIATION OF HEALTH PLANS, Washington, D.C.

1997

*Library Assistant*

- Ordered material, filed journals, researched current health news

UNITED STATES DEPARTMENT OF AGRICULTURE, Beltsville, MD

1994-1995

*Lab Research Assistant*

- Prepared and tested fluids from Holstein dairy cows for collaborative research project

## TEACHING EXPERIENCE

### WEST VIRGINIA UNIVERSITY

DEPARTMENT OF BIOLOGY, Morgantown, WV

2004-2006

*Teaching Assistant for Biol 115 Introduction to Biology* (2004, 2005)

*Teaching Assistant for Biol 321 Total Science Experience in Ecology* (2005)

*Teaching Assistant for Biol 106 Environmental Biology* (2005)

*Teaching Assistant for Biol 361 Plant Ecology* (2006)

REGIONAL MATH/SCIENCE CENTER  
of FROSTBURG STATE UNIVERSITY, Frostburg, MD  
*Science Teacher*

2004

- wrote curriculum and taught hands on environmental science and statistics to high school student of varied abilities

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EDUCATION AND HONORS

WEST VIRGINIA UNIVERSITY, Morgantown, WV  
Ph.D. in Biology

2007

Major: Ecology and Evolutionary Biology

Dissertation: Land use and forest productivity in the Central Appalachian region

- Attained 4 Doctoral Student Research Awards
- Received 3-year Eberly Student Stipend Enhancement

FROSTBURG STATE UNIVERSITY, Frostburg, Maryland

B.A. in Wildlife and Fisheries

1999

Major: Wildlife Management

Minors: Biology and Spanish

Extra studies: Environmental Issues in Ecuador (1998), Meteorology for Weather Education (2000), Calculus II- III (2001-02), Web page design (2001), Physics I -II (2001-02), Ecological

and Environmental Science Issues graduate seminar (2002)

- Graduated with honors
- English Colloquium invitation
- Service Leadership Award Nomination
- 3 undergraduate academic scholarships
- Study abroad scholarship

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PUBLICATIONS

*Publication in press:*

Parker, D., A. Hessel, and **S. Davis**. 2007. Complexity, spatial modeling, and the human dimension: fundamental challenges for mapping unknown outcome spaces. *Geoforum* Special Issue "Biocomplexity in Coupled Human-Natural Systems."

*Publication in review:*

**Davis, S.C.** and R.B. Thomas. 2007. Productivity of nitrogen saturated forests in the Central Appalachian region: an adaptation of the PnET-CN model. *Ecological Modelling*.

*Publications in preparation:*

**Davis, S.C.**, A.E. Hessel, and R.B. Thomas. Harvest history and terrestrial carbon budgets of Central Appalachian forests. *Global Change Biology*.

**Davis, S.C.**, K.E. Dragan, C.R. Buyarski, R.B. Thomas. Spatial consistency of foliar nitrogen concentrations in Central Appalachian forests. *Ecosystems*.

**Davis, S.C.**, J. Mohan, and R.B. Thomas. Photosynthetic responses of *Vitis rotundifolia* and

*Lonicera japonica* growing in a forest ecosystem with elevated atmospheric carbon dioxide and nitrogen fertilization. Global Change Biology.

#### PRESENTATIONS

- Davis, S.C.**, A. E. Hessel, R B. Thomas. 2007. Productivity of nitrogen saturated forests in the Central Appalachian region: an adaptation of the PnET-CN model. Eberly College Poster Session, Morgantown, WV.
- \*Briden, S.C.D.**, A.E. Hessel, and R.B. Thomas. 2006. Effects of disturbance on the terrestrial carbon budget of a Central Appalachian forest: an evaluation of the PnET-CN model. Ecological Society of America Meeting, Memphis, TN.
- \*Briden, S.C.D.**, A.E. Hessel, W. Peterjohn, and R. Thomas. 2006. Effects of disturbance on the terrestrial carbon budget of a Central Appalachian forest. American Geophysical Union, 2006 Joint Assembly, Baltimore, MD.
- \*Briden, S.**, M. Adams, A. Hessel, W. Peterjohn, and R. Thomas. 2005. Foliar nitrogen concentrations of deciduous hardwood trees along an elevation gradient in West Virginia. West Virginia Academy of Science Meeting, Morgantown, WV.
- \*Briden, S.** and R. Thomas. 2005. Photosynthetic responses of two vine species, *Vitis rotundifolia* and *Lonicera japonica*, growing in a forest ecosystem with elevated atmospheric carbon dioxide. Ecological Society of America Meeting, Montreal, QC.
- \*Briden, S.**, A. Hessel, D. Parker, W. Peterjohn, and R. Thomas. 2005. Linking ecosystem and socioeconomic models: land use and carbon storage in West Virginia. Eberly College Poster Session, Morgantown, WV.

*\*Please note that my previous legal name was Briden and that Davis is legally my name as of December 2006.*

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#### COMPUTER SKILLS

- Word, Excel, Powerpoint, Access databases
- Adobe Photoshop, Adobe Premiere (video editing), Dreamweaver web design,
- Visual Basic, JavaScript
- SAS-JMP

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#### ADDITIONAL TRAINING AND EDUCATION

- Meteorology for Weather Education, Spring 2000
- Orientation Teaching Workshop, August 2000
- Dreamweaver Workshop, November 2000
- Access Workshop, November 2000
- Dimensions of Learning Workshop, January 2001
- Advanced Dreamweaver Workshop, January 2001
- Renewable Energy and Sustainable Living Fair Workshops, June 2001
- Energizing Schools (NESEA), October 2001

- Grant Writing Workshop, October 2002

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PROFESSIONAL MEMBERSHIPS AND SERVICE ACTIVITIES

- Ecological Society of America (current)
  - Expanding Your Horizons
  - Nature Conservancy
  - Alternative Break at FSU (Coordinator)
  - Earth Day (Coordinator)
  - Wildlife Society FSU Chapter
  - Americorps Read to Succeed
-